1995

Feeding ecology of the basking shark (Cetorhinus maximus) relative to distribution and abundances of prey

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FEEDING ECOLOGY OF THE BASKING SHARK (*CETORHINUS MAXIMUS*) RELATIVE TO DISTRIBUTION AND ABUNDANCE OF PREY

A Thesis Presented to
The Faculty of Moss Landing Marine Laboratories
San Jose Sate University

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science
San Jose State University

By
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May 1995

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ABSTRACT

FEEDING ECOLOGY OF THE BASKING SHARK
(*CETORHINUS MAXIMUS*) RELATIVE TO DISTRIBUTION
AND ABUNDANCE OF PREY

The relationship between prey availability and presence of basking sharks feeding at the surface was determined by collecting zooplankton near and away from feeding basking sharks. Zooplankton density in basking shark feeding areas was significantly greater (4-42 times) than away from feeding areas in Monterey Bay (one-tailed paired t-test, n=5, p=0.016) and Santa Barbara Channel Islands (n=1). There were no differences in zooplankton density near and away from basking sharks sighted at the surface in Clayoquot Sound, B.C. (power=97%) and the Gulf of Maine (power=63%). A calanoid copepod, *Calanus pacificus*, was the most important prey item in Monterey Bay, British Columbia, and the Santa Barbara Channel Islands. *Calanus finmarchicus*, was the most important taxon found in feeding areas in the Gulf of Maine. Calanoid copepods *Metridia longa*, *Calanus hyperboreus*, and *C. finmarchicus* were the most important prey items identified from nine basking shark stomach contents collected off Saint John's, Newfoundland. In Monterey Bay, peak basking shark abundance corresponded with greater zooplankton abundance in May, August, and November. Increased basking shark sightings in nearshore regions relative to offshore regions corresponded with greater zooplankton abundance nearshore than offshore between 1991 and 1992. Therefore, basking sharks may move into surface waters for feeding and possibly for other purposes.

ACKNOWLEDGMENTS

I respectfully thank the members of my thesis committee for their continual support and editorial comments which greatly improved the quality of this document. They are my major advisor, James T. Harvey, Gregor M. Cailliet, and Nicholas A. Welschmeyer of Moss Landing Marine Laboratories (MLML) and Michael M. Mullin, of Scripps Institute of Oceanography. Special thanks to Jim Harvey for finding time for me among the 25 graduate students he advised during my tenure in his lab.

Funding for this project was provided by the following organizations: Dr. Earl and Ethel Myers Oceanographic and Marine Biology Trust, Lerner-Gray Fund of the Museum of Natural History, David and Lucile Packard Foundation, Clayoquot Biosphere Project, Allied Whale, and Bill Peterson.

The following people offered equipment and/or logistical support. Kris Wright helped with sampling in British Columbia. Dawn Outram and Tom Norris helped with zooplankton surveys. Many students at MLML participated in the zooplankton surveys, searched for and swam with basking sharks with me and I thank them sincerely. Many students also critically reviewed several versions of the thesis draft. Valerie Loeb (MLML), Steve Katona (Allied Whale), and Enric Cortes (Mote Marine Lab) thoroughly reviewed the draft and offered helpful suggestions. Captain Tracy Thomas piloted the R/V Ed Ricketts for zooplankton surveys. Jim Darling and Josie Cleland at Clayoquot Biosphere Project provided vessel use and housing in British Columbia. Ann Zoidis and others of Allied Whale collected the samples from the Gulf of Maine. HaeJin Jeong counted *Calanus pacificus* from samples collected off the Santa Barbara Channel Islands. Alan Baldridge, formerly of Hopkins Marine Station, and Robert Lea, Department of Fish and Game, provided historical basking shark sighting information. Mark Ohman, Anne Townsend, and Margaret Knight (Scripps Institute of Oceanography) identified and verified identifications of copepods, euphausiids, and zoea from zooplankton samples. Jon Lien provided basking shark stomach contents from St. John's Newfoundland. The Pelagic Shark Research Foundation (Sean VanSommeran) promptly contacted me regarding the locations of basking shark sightings. Aldo DeRose helped me build and fabricate equipment. The MLML librarians were most helpful with literature

searches. They are Sheila Baldridge, Sandy O'Neil, Joan Parker and Valerie Murphy.

I have met many special friends during my tenure at Moss Landing Marine Labs and wish to thank them for sharing the joys and trials of being a graduate student at MLML. Tom Norris has been a wonderful friend and companion with whom I have shared many great times. Doreen Moser, Debbie Nebenzahl, and Tricia Lowe were wonderful housemates during our occupancy in John Oliver's Slough House. Also, I will never forget many joyous times and sunsets at the Blue House in Moss Landing.

I wish to extend a special thank you and love to my family, Mom (Jackie B.) and Dad (Capt. Bob), my sister Donna, and my brother Bobby for their moral support. My mother and father introduced me to the marine environment, provided me with the opportunity to grow up around and in it, and have continually encouraged me to have confidence in myself to pursue a career in marine science. I have and will continue to do so.

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INTRODUCTION

The basking shark (*Cetorhinus maximus*, Gunnerus) is the second largest fish species, reaching a maximum total length of 12.2 to 15.2 m (Compagno 1984), exceeded in size only by the whale shark (*Rhincodon typus*). There have been few scientific observations of this species and few accounts of its related fisheries, primarily because large animals are not very abundant and because basking sharks are rarely observed feeding in nearshore surface waters. Current knowledge about this species is based upon commercial catches from Scotland and Norway, from incidental capture in nets, from stranded individuals, and from seasonal sightings in nearshore surface waters (Kunzlik 1988).

Most information gathered about basking sharks has resulted from observations of basking sharks sighted seasonally at the surface. Three explanations have been proposed to explain seasonal appearance of basking sharks in nearshore surface waters. First, appearance of basking sharks in surface waters is associated with seasonally high plankton productivity (Kunzlik 1988). The second explanation relates to a correlation between water temperature and seasonal occurrence of basking sharks (Squire 1967, Owen 1984, Lien and Fawcett 1986). The third relates basking shark occurrence in surface waters to courtship behavior in this species (Matthews 1950, Maxwell 1952, Watkins 1958). For several reasons, I chose to examine prey distribution and abundance when basking sharks were observed feeding at the surface.

First, when basking sharks are observed seasonally at the surface, they are frequently sighted with their mouth agape (personal observation), indicating they are probably feeding. Individuals or large groups (up to 1000 individuals) of basking sharks have been observed filter-feeding on zooplankton patches in surface coastal waters of amphitemperate regions along both coasts of North America, from Newfoundland to Florida, and from Gulf of Alaska to the Gulf of California (Squire 1991). Basking sharks feed by swimming with their mouth agape (approximately 1 m diameter), with gill rakers erect, forming a sieve that filters zooplankton from the water (Hallacher 1977, Kunzlik 1988). Gill rakers may reach 15 cm length and extend across the gaps between the five gill arches when the sharks feed. There are 1,000 to 1,300 rakers per 70 cm gill arch. After approximately 30 to 60 seconds of filtering, a shark will periodically close its mouth, rakers will collapse, and all filtered material will be collected by a mucus coating which is secreted by glands at the base of the rakers (Hallacher 1977, Kunzlik 1988). When cruising at a constant speed of 2 knots, an average adult filters approximately 2000 tons of water/hour (Compagno 1984). The basking shark differs from the other two filter-feeding sharks, the megamouth (*Megachasma pelagios*) and whale shark, in that it relies entirely on passive water flow created by swimming (Compagno 1984). The other two filter feeders actively pump or gulp water and prey.

Secondly, the behavior and movements of large vertebrates is often most closely linked to reproduction and food. Courtship behavior, however, is difficult to observe. The presence of prey was a testable explanation for the occurrence of large congregations of basking sharks at the surface.

Few researchers have documented prey items from the gut contents of basking sharks. Sproston (1948) recorded *Calanus sp., Pseudocalanus sp., Oithona sp.* copepods, and decapod larvae from basking shark stomach contents. Matthews and Parker (1950) reported copepods, including *Calanus sp.*, fish eggs, *Cypris* larvae, and decapod larvae (zoea, megalopa). No prey items larger than *Calanus* were found inside the gut. Parker and Boesman (1954) found *Calanus sp., Sagitta,* and fish eggs in basking shark stomachs. Antezana (1977) found pelagic larvae of the mole sand crab (*Emerita analoga*), *Rhincalanus sp.* copepods, decapods, and stomatopods of 5 to 25 mm length in gut contents of a basking shark caught off Chile. Based on gut contents from a basking shark incidentally caught off Japan, Mutoh and Omori (1978) concluded that the shark was feeding at night on oceanic shrimps (*Sergestes similis*, 40 to 54 mm body length) at depths below 100 m.

Several researchers have studied the relationships between large marine vertebrate predators and prey availability. During May 1986, Wishner et al. (1988) demonstrated most of the northwest Atlantic right whale population fed on a large monospecific aggregation of *Calanus finmarchicus* copepods, copepodite stage IV (C IV), in the Great South Channel off New England. The whales and copepod layer were located 20 km north of the 100 m depth contour on the warmer side of a thermal front. An average of 41,600 copepods/m^3 was found inside the copepod patch. *Calanus finmarchicus* abundance inside the patch was 311 times greater than immediately adjacent to the patch, and 83 times greater than immediately below the patch. In 1988 and 1989 in the Gulf of Maine, Wishner et al. (1995) recorded greater abundance and relative proportions of older copepod life stages (C III-C IV) in the water column near feeding right

whales compared with areas without whales. Abundance of *C. finmarchicus* and copepod biomass in the total water column, however, did not differ always between areas near and away from feeding whales. They suggested whales sought out aggregations of older copepod life stages (C III-C IV) rather than the most dense aggregations (Wishner et al. 1995).

Schoenherr (1989) determined blue whales fed on dense patches of euphausiids, *Thysanoessa spinifera,* both at the surface during daytime swarms and in deep scattering layers along the southeast edge of the Monterey Submarine Canyon, California. *Thysanoessa spinifera* comprised 64.4% of the total zooplankton biomass at the surface in whale feeding areas, whereas surface tows taken away from whale feeding areas consisted of only 0.3% euphausiids.

Several researchers have recorded basking sharks feeding in dense patches of zooplankton, but none sampled the zooplankton when sharks were feeding at the surface. Bigelow (1926) concluded from observations in the Gulf of Maine that copepods probably were the primary prey item for basking sharks. Ruud (1929) observed basking sharks feeding on swarms of *Calanus* copepods in the Firth of Forth, Norway, on three occasions, once in March and twice in July. Most recently, Owen (1984) reported that monthly sightings of basking sharks (sharks/per unit effort) in New England waters correlated more closely with *Calanus finmarchicus* abundance than with total zooplankton abundance, other copepod taxa, or prey abundance in other areas in New England waters. Detailed in situ observations of the behavior of surface aggregations of *C. finmarchicus* have been made only by Bainbridge (1952). He described two distinct zones of *C. finmarchicus*. In the upper 0.3 meter, there were large concentrations of *C. finmarchicus*, which were aggregated in numerous small

groups (approximately 12 individuals) that swam around one another on the underside of the surface film. Below this upper zone, copepods were less concentrated, more evenly distributed, and swam steadily upward or downward at least 1.5 to 1.8 meters. Although these researchers observed basking sharks feeding in copepod patches, this study was the first attempt to quantify prey distribution and abundance near and away from surface feeding basking sharks.

The main objective of this study was to determine the relationship between prey availability and occurrence of basking sharks feeding at the surface. Of particular interest was whether basking sharks fed in large prey concentrations when feeding at the surface. This was accomplished by measuring zooplankton distribution and abundance near and away from feeding areas of basking sharks. Additionally, the relative importance of zooplankton taxa, which constitute the diet of basking sharks, was determined. I hypothesized there would be greater abundance of zooplankton inside than outside basking shark feeding areas if basking sharks were feeding optimally in dense zooplankton aggregations and that these dense aggregations would be comprised of one or few relatively important taxonomic groups. Therefore, zooplankton distribution outside feeding areas would be more diverse than within feeding areas.

METHODS

Study Sites

Zooplankton tows were conducted among basking sharks feeding at the surface in four locations. In December 1991, zooplankton were collected in basking shark feeding areas just offshore Santa Cruz, in Monterey Bay, California

(36°55.8' N, 122°03.7' W; Fig. 1) in water depths of 15.2 to 30.5 meters. Additionally, on 14 February 1991, zooplankton were collected opportunistically near feeding basking sharks approximately two km west of Fort Ord, Monterey Bay. All feeding events occurred over the continental shelf, which extends approximately three kilometers off the sandy beach and rocky cliffs of central California. There also is a large submarine canyon which begins approximately 100 m offshore Moss Landing Harbor and reaches approximately 1830 m depth. This area is exposed to the Pacific Ocean, and is characterized by predominantly northwest winds and moderate ocean swell.

From June to September 1993, net tows also were conducted in Clayoquot Sound near Flores Island, a large island on the Pacific coast of Vancouver Island, British Columbia, in the waters of Sydney and Shelter Inlet (49°70.0' N, 126°30.0' W; Fig. 2). Shelter Inlet is completely protected from the open ocean and Sydney Inlet opens into the Pacific. The inlets are characterized by steep cliffs and shorelines that slope into water of 50 to 160 m depth. This area is subjected to relatively strong tidal currents.

From August to September 1993, prey were collected in approximately 7.0 to 71.0 m water depth within a 3.2 km radius of Mount Desert Rock, a 1.42 km^2 island located 33.8 km south of Mount Desert Island in the Gulf of Maine (43°06.0' N, 68°05.7' W; Fig. 3). Local tidal currents transport deep (183 m) water against the island's shoals, producing turbulence and upwelling of nutrient rich water.

Finally, on 27 April 1989, an additional sample was obtained opportunistically from an oceanographic station (CalCOFI Cruise 8904) where basking sharks were feeding at the surface in water of 30 m depth. This station is

located north of Santa Cruz Island, Santa Barbara Channel Islands, California (34°13.5' N, 119°24.7' W; Fig. 4).

Zooplankton Tows Collected in Basking Shark Feeding Areas

Three replicate zooplankton tows were conducted alongside each surface feeding shark within fifteen minutes (usually less than five) of when the shark was last sighted. These tows were considered "inside feeding area" tows. Subsequently, three tows were conducted at a random heading greater than 0.5 km (usually 0.5-1.0 km) away from where the shark was last sighted. These tows were considered "outside feeding area" tows. This sampling scheme was conducted during all eight feeding events observed in Clayoquot Sound, B. C. and four of five feeding events observed in Monterey Bay. Two replicate tows were conducted both inside and outside feeding areas on one occasion in the Gulf of Maine and only one tow was conducted on the remaining three occasions in the Gulf of Maine.

In Monterey Bay and British Columbia, these zooplankton tows were conducted in the upper 1 m of water using a 500 μm, 1-m mouth diameter plankton net (Research Nets, Inc.; Omori and Ikeda 1984). This is the same area of water used by basking sharks when feeding at the surface. A 335 μm, 0.25 m diameter plankton net was used to collect zooplankton in the Gulf of Maine. These mesh sizes were chosen because they filter prey items of the same size found in basking shark stomach contents (Sproston 1948, Matthews and Parker 1950, Parker and Boesman 1954, Mutoh and Omori 1978). A pre-calibrated flow meter (General Oceanics Model 2030) was mounted at the mouth of the net to reliably estimate water volume filtered per one to five minute tow.

Samples from horizontal surface tows were preserved in approximately 10% formalin in sea water. Upon return to the lab, each tow was subsampled twice using a Stempel pipette (1-40 ml), enumerated, and individual zooplankton identified to the lowest taxon possible. Zooplankton density (number of individuals/m^3 water volume filtered) was calculated by multiplying average number of individuals counted per subsample by total replicate tow volume and dividing by the water volume filtered during that tow.

Zooplankton were collected opportunistically off the Santa Barbara Channel Islands during an oceanographic survey (CalCOFI cruise), 17-30 April 1989. An oblique net tow was conducted from 26 m depth to the surface using a 71-cm mouth diameter paired bongo net with 505 µm mesh net. Water volume filtered was calculated from flow meter readings. One sample per pair was retained and preserved. Only *Calanus pacificus* copepods (adults and copepodite stages) were identified and enumerated. All other zooplankton were quantified as "other".

The first attempt to associate basking sharks feeding at the surface with dense aggregations of prey was conducted by correlating shark abundance and zooplankton density. Because the frequency distribution of sharks and prey was non-normal, Spearman rank correlation was used to determine if zooplankton abundance and number of sharks sighted feeding at the surface were correlated for all feeding events.

Additionally, one-tailed paired t-tests were conducted for Monterey Bay, CA, Clayoquot Sound, B.C., and the Gulf of Maine, to determine if there were significant differences between density of zooplankton inside and outside feeding areas of basking sharks (Zar 1984). A posteriori, power analyses were

conducted on all paired t-tests in which the null hypothesis was not rejected (Zar 1984).

Because variances were unequal and distributions were non-normal, a modified two-way Kruskall-Wallis was conducted to compare the relationship of zooplankton abundance among the four study sites (Monterey Bay, Clayoquot Sound, B.C., the Gulf of Maine, and off the Santa Barbara Channel Islands) and proximity to sharks (inside and outside; Systat, 1992). Subsequently, power of the tests was determined if the null hypotheses were not rejected (Zar 1984).

The zooplankton diversity inside and outside basking shark feeding areas also was quantified. The differences in abundance among several zooplankton taxa from inside and outside basking shark feeding areas were compared by calculating a Modified Index of Relative Importance (MIRI) for each prey taxon. Usually, percent number (%N), percent volume (%V), and frequency of occurrence (% FO), are combined to form the IRI index for each taxon (Pinkas et al. 1971, Kurian 1977). Because it was not possible to estimate %V for each individual enumerated in this study, only %N and %FO were used to calculate the MIRI (App. 1). Additionally, an individual MIRI was calculated for each zooplankton tow. A mean MIRI was calculated for all inside and outside tows and these means were averaged to form a mean MIRI for each taxon. By calculating individual MIRI's for each tow, the variability in mean number of taxa per tow was used in the combined MIRI calculation. This reduced the possibility that an unusually large MIRI may have been calculated for a potential prey item, thus making it appear important, when it was extremely abundant in only one or a few tows.

Zooplanktonn density was compared statistically between location (inside and outside feeding areas) and taxa for three study sites (Monterey Bay, British Columbia, and Gulf of Maine) using a two-way modified Kruskall-Wallis test. A posteriori, paired t-tests and power analyses were conducted to compare inside and outside densities for each taxon (Zar 1984). Only taxa with average densities >5.0 individuals/m^3 were compared using paired t-tests.

Several overlap indices, including Shannon-Wiener diversity, dominance, and zooplankton evenness, were calculated to compare potential prey inside and outside feeding areas of basking sharks. (Kohn 1968, Levin 1968, Fager 1972, Pielou 1975;
App. 1).

Similar to the method in which MIRI's were calculated, Mean Percent Similarity Indices (PSI), Mean Morisita-Horn, and Mean Horn Indices were calculated by averaging proportional and abundance (number/m^3) values per tow for each taxon (App. 2). These indices were calculated using the Krebs Fortran Program, "Similar" (Krebs 1989). Ricklefs and Lau (1980) determined these indices were least biased with regard to sample size and prey unevenness. As suggested by Cailliet and Barry (1979), several indices were calculated .

To determine if sample size was adequate for each study site, cumulative species curves were created by generating 1000 randomized arrangements of the sample data for zooplankton tows collected inside and outside feeding areas of basking sharks in Monterey Bay, British Columbia, and Maine . Similarly, cumulative species curves were generated for several zooplankton subsamples in each area to determine if subsample size per replicate tow was adequate.

Food Habits

Direct evidence of prey eaten by basking sharks was determined by examining stomach contents. Sixteen stomach contents of basking sharks were obtained from Jon Lien, Whale Research Group (n=15), in Newfoundland, and Allied Whale (n=1), in the Gulf of Maine. Prey taxa were identified from nine stomach contents from basking sharks entrapped in salmon nets and cod traps in Newfoundland. Whole exoskeletons could be identified from only two samples and thus, only two reliable density estimates could be determined.

Modified Index of Relative Importance values were calculated for each prey taxon found in the stomach contents. These MIRI values were compared to the MIRI values for the four study sites where zooplankton tows were collected inside feeding areas of basking sharks.

RESULTS

Basking Shark Distribution and Prey Abundance in Feeding Areas

Five basking sharks were observed feeding at the surface simultaneously during four feeding events in Monterey Bay in December 1991. Four basking sharks were observed feeding at the surface during an additional feeding event on 13 December 1991 in Monterey Bay. On 14 February 1991, approximately six to eight basking sharks were observed feeding at the surface off Fort Ord, Monterey Bay, when zooplankton were collected opportunistically. In Clayoquot Sound and in the Gulf of Maine, only one shark/event was observed feeding at the surface during most feeding events. Two basking sharks were observed surface feeding on 17 June 1993 in British Columbia. Approximately 20 basking sharks were observed feeding at the surface simultaneously on one occasion off

the Santa Barbara Channel Islands in April 1989.

Zooplankton abundance was measured inside and outside feeding areas of basking sharks on 18 occasions in Monterey Bay (n=5), Clayoquot Sound, B.C. (n=8), the Gulf of Maine (n=4), and off the Santa Barbara Channel Islands, California (n=1). There was a significant positive correlation between maximum number of sharks sighted feeding at the surface and mean zooplankton abundance collected inside the feeding areas during each feeding event. (r_s=0.68, n=18, p<0.002; Fig. 5).

Zooplankton density inside feeding areas of basking sharks was significantly greater than outside feeding areas in Monterey Bay ($t_{one\text{-}tailed}$=3.21, n=5, p=0.016; Fig. 6). The greatest density of zooplankton measured inside feeding areas of basking sharks was 2647 individuals/m^3 water volume filtered. Zooplankton abundance was not estimated for the opportunistic sample collected in Monterey Bay on 14 February 1991 because water volume filtered per tow could not be calculated. Although zooplankton abundance was greater inside feeding areas during four of eight events in Clayoquot Sound, the differences in mean densities between inside and outside feeding areas were not significant ($t_{one\text{-}tailed}$=-0.16, n=8, p=0.440; Fig. 7). The statistical power of detecting differences between zooplankton density inside and outside feeding areas in British Columbia was 97%. In Clayoquot Sound, the greatest density measured inside feeding areas of basking sharks was 739 individuals/m^3 water volume filtered. In the Gulf of Maine, zooplankton density was greater inside than outside feeding areas on two of four events. There was no significant difference, therefore, among combined results from all occasions in the Gulf of Maine ($t_{one\text{-}tailed}$=-0.41, n=4, p=0.353; Fig. 8). There was only 63% power of

detecting a difference between inside and outside feeding areas in Maine. The greatest density of zooplankton measured inside feeding areas of basking sharks in Maine was 1883 individuals/m^3 water volume filtered. Mean zooplankton abundance at the station where numerous sharks were feeding off the Santa Barbara Channel islands was 4.5 times greater than at a station ten km away from feeding sharks (2234 individuals/m^3 inside, 462 individuals/m^3 outside, n=1).

There was no significant difference in zooplankton abundance among the four study sites (Monterey Bay, British Columbia, the Gulf of Maine, and off the Santa Barbara Channel Islands; H=3.33, n=4, p=0.100) nor between inside and outside feeding areas (H=3.00, n=18, p=0.100) or for the interaction term (H=0.66, n=34, p<0.500). Mean zooplankton abundance measured inside feeding areas, however, was greater in Monterey Bay and off the Santa Barbara Channel Islands than in British Columbia and the Gulf of Maine (Fig. 9). The power for detecting differences between inside and outside tows was 68%, 55% power for detecting differences among study sites, and 80% power for detecting a significant interaction term among the two factors, location of zooplankton tow and study area.

Zooplankton Diversity In Feeding Areas of Basking Sharks

Ninety-six taxa were identified from Monterey Bay (n=33), British Columbia (n=44), and Gulf of Maine (n=19; Table 1). *Calanus pacificus* was the only taxon enumerated for the Santa Barbara Channel Islands sample.

A cumulative taxa curve was generated for each series of zooplankton tows inside and outside feeding areas of basking sharks in Monterey Bay, British Columbia, and Maine (Figs. 10-12). In Monterey Bay, the curve was not asymptotic; therefore, the number of tows conducted inside and outside the

feeding areas do not appear sufficient for identifying all potential prey taxa (Fig. 10). The sample size does not appear sufficient for identifying zooplankton collected from zooplankton tows inside and away from feeding areas in British Columbia (Fig. 11). In the Gulf of Maine, sample size clearly is insufficient for identifying potential prey collected inside and outside feeding areas of basking sharks (Fig. 12). The cumulative species curve generated for number of subsamples per zooplankton tow indicates two subsamples/tow was adequate for the Gulf of Maine and possibly for Monterey Bay and British Columbia (Fig. 13). The most important potential prey items, however, were documented for all zooplankton tows and only rare taxa may have been missed.

The Mean Modified Indices of Relative Importance (MIRI's) were compared among taxa between inside and outside feeding areas for four study sites (Tables 2-4). Ten taxa with the greatest MIRI values were visually depicted (Figs. 14-16). *Calanus pacificus* was the most important (greatest MIRI value) taxon among all study sites along the west coast of North America. *Calanus finmarchicus* was the most important taxon in the Gulf of Maine. Similarly, *C. pacificus* copepods were more important inside than outside feeding areas for the west coast of North America and *Calanus finmarchicus* copepods were more important inside feeding areas in the Gulf of Maine (Figs. 14-16). *Acartia sp.* also was more important inside than outside feeding areas in British Columbia and the Gulf of Maine (Figs. 15-16). All remaining taxa usually were relatively more important outside than inside feeding areas. (Tables 2-4).

There was a significant interaction between location (inside and outside feeding sharks) and taxon for three study sites (Monterey Bay, British Columbia, and Maine; Kruskall-Wallis test). Off the Santa Barbara Channel Islands and in

Monterey Bay, densities of *C. pacificus* were significantly greater inside than outside feeding areas ($t_{one\text{-}tailed}$=2.61, n=6, p=0.024, Monterey Bay; Table 5). Additionally, in Monterey Bay, chaetognaths were significantly greater inside than outside feeding areas ($t_{one\text{-}tailed}$=21.64, n=6, p=1.95 x 10^{-6}). There were no significant differences in abundance of the most important taxa, *C. pacificus* and *Acartia* in British Columbia, and *C. finmarchicus, Centropages sp.*, and *Acartia sp.* in the Gulf of Maine between inside and outside feeding areas (Tables 5-6). The power for detecting differences in abundance of both *C. pacificus* and *Acartia sp.* between zooplankton tows inside and outside feeding areas in British Columbia was 99%. The power of detecting differences in abundance of *C. finmarchicus* between inside and outside zooplankton tows in Maine was 89%, for *Centropages sp.* it was 92%, and for *Acartia sp.* it was 99%. In British Columbia, three taxa were significantly more abundant inside than outside feeding areas, but these taxa were less important prey items than the dominant taxon, *C. pacificus* (Table 5). In the Gulf of Maine, no taxa were significantly more abundant inside than outside feeding areas (Table 6).

Several overlap indices, including Shannon-Wiener diversity, dominance, and zooplankton evenness yielded similar trends among Monterey Bay and the Gulf of Maine. In Monterey Bay and Maine, diversity and zooplankton evenness were greater outside than inside feeding areas (Table 7). Consequently, dominance was greater inside than outside feeding areas (Table 7). In Clayoquot Sound, all three values were greater inside feeding areas.

Off Santa Barbara, *C. pacificus* was the dominant zooplankton taxon (dominance index of 98%) at the station where sharks fed at the surface versus 90% dominant at a station 10.3 km away from where sharks fed (Table 8). Also

the dominance and density of *C. pacificus* at the station where sharks fed was much greater than other seasons of the year when the station was sampled and no sharks were observed (Table 8).

Mean Percent Similarity Index (PSI), Mean Morisita-Horn, and the Mean Horn similarity indices indicated that zooplankton inside and outside feeding areas were similar (value >0.65 =similar) in most cases for the three areas (Monterey Bay, British Columbia, and Maine; Table 9). There were only two cases where zooplankton inside and outside feeding areas were dissimilar: 1) when relative proportions (p^i) were used to calculate mean PSI values for Monterey Bay and 2) when densities (number/m3) were used to calculate PSI, Morisita-Horn, and Horn values for the Gulf of Maine (Table 9).

Food Habits

All stomach samples collected off St. John's, Newfoundland, and in the Gulf of Maine contained broken exoskeletons from crustaceans. Whole copepods and other taxa were obtained from nine stomachs from Newfoundland. Seven of nine stomach contents contained greater than 30% unidentifiable broken exoskeletons. Fourteen taxa were identified from the nine stomach contents containing whole exoskeletons. *Metridia longa*, a calanoid copepod, had the greatest MIRI value of all prey items found in the gut contents (Table 10). *Calanus hyperboreus* and *C. finmarchicus* also were relatively important prey items (Table 10, Fig. 17).

Density estimates (3.58×10^7 and 1.67×10^7 individuals/m3) were determined from two stomach contents in which *C. hyperboreus* and *C. finmarchicus* were the most important prey items (i.e. greatest MIRI values). These density estimates are considerably greater (>10^4 individuals/m^3 greater)

than densities of zooplankton recorded from zooplankton tows collected in feeding areas of basking sharks in Monterey Bay, the Santa Barbara Channel Islands, Clayoquot Sound, and the Gulf of Maine.

DISCUSSION

Sampling and Experimental Design

There are many difficulties associated with in situ quantitative measurements of zooplankton abundance. Scientists have dealt with difficulties such as net avoidance, replication, plankton patchiness, net size discrimination, towed water volume estimates, and other limitations of quantifying zooplankton abundance since the first plankton tow was conducted. Net avoidance probably was not a major problem in this study because net tows were conducted at two knots, the same speed as average swimming rate of basking sharks. Also, all nets were white mesh, the same color as the inner lining of the basking shark mouth. Nets were used to collect prey items with similar mesh sizes to the sizes of prey identified from basking shark stomach contents .

Some aspects of the experimental design of this project could have been improved. This project was designed to test whether prey densities inside and outside feeding areas of basking sharks differed using a paired t-test. Three replicates were conducted in one area inside and one area outside of feeding basking sharks. This approach was designed to reduce the variability among replicates. A random direction and position greater than 0.5 km away from a feeding shark was chosen for tows conducted outside the feeding area. The limitation of this design is that due to the small spatial coverage, the low number of samples collected may not have been representative of the entire study area.

The areas both inside and outside feeding basking sharks should have been sampled more intensively spatially to determine zooplankton distribution in the area. Also, a rough estimate of patch dimensions may have been obtained using a more randomized and intensive sampling scheme.

Plankton patchiness also may have influenced the results of this study. Plankton is distributed patchily along both large and small temporal (minutes to years) and spatial scales (5 cm to 3,000 km; Cassie 1959, 1962). In feeding areas of right whales, abundance of *C. finmarchicus* varied by a factor of 1 to 890 times in zooplankton tows spanning 0.5 to 1.5 km and by a factor of 1 to 50 times during a 24-hour period in the same region (Wishner et al. 1995). Possibly, zooplankton abundance estimates calculated for this study were overestimated if net tows were conducted among patches or underestimated if net tows were conducted between patches. I believe, however, estimates of zooplankton abundance collected inside feeding areas were reasonable.

With recent advances in acoustical technology, it would have been possible to quantify zooplankton density within the entire area using high frequency bioacoustic equipment, and the density estimates could have been verified with net tows. This would reveal patch dimensions both inside and outside feeding areas of basking sharks. This, however, was not accomplished due to financial limitations and may be difficult to pursue due to the proximity of basking sharks feeding at the surface. Wishner et al. (1988) used a 200 kHz Biosonics acoustic system to measure the abundance of zooplankton at one second intervals in feeding areas of right whales . They quantified patch dimensions and designated three distinct regions in and near the patch in the Great South Channel: the patch itself, the water column below the patch, and the

region immediately adjacent to the patch. The *Calanus finmarchicus* layer covered 2500 km^2 and remained several days. Use of a hydroacoustics system would have greatly enhanced the ability to describe the distribution and abundance of prey in this project.

Every effort was made to sample near the feeding shark or in the immediate area where the shark was sighted, and to avoid sampling the depleted area where the shark had fed. Because the water mass was not marked, this was difficult to accomplish. It is possible, that due to strong currents, a different area of water was sampled than the area in which the shark fed. The zooplankton abundance could have been different between the two water masses.

Replicate sampling probably was inadequate for identifying rare species in Monterey Bay, British Columbia, and the Gulf of Maine (Fig. 13-15). The number of subsamples per net tow probably was adequate for the Gulf of Maine, however, inadequate for identifying rare species in Monterey Bay and British Columbia (Fig. 16). I believe, however, the most abundant potential prey items were identified from all sampling areas and only rare, less abundant taxa were missed.

From the results of the mean MIRI's, *Calanus* sp. was relatively more dominant inside than outside feeding areas of basking sharks for all study sites. *Calanus* sp. also was a dominant prey item identified from the stomach contents. Clearly, *Calanus sp.* are important prey items for basking sharks. Small sample size and zooplankton unevenness may have influenced the results of the diversity indices which were calculated inside and outside feeding areas of basking sharks. Ricklefs and Lau (1980) demonstrated using computer simulation that the sampling distributions of all measures of niche overlap are

strongly affected by sample size, number of prey items, and evenness of resource. Horn's index of similarity was the least biased of all three factors. Smith and Zaret (1982) reported the Morisita-Horn index was the best overlap measurement with nearly zero bias for all sample sizes and when there is a large number of taxa.

Feeding Behavior of Basking Sharks

When groups of basking sharks were observed feeding at the surface in Monterey Bay and off the Santa Barbara Channel Islands, they fed on dense copepod patches consisting mainly of *C. pacificus*. Zooplankton density was 4 to 42 times greater inside feeding areas of basking sharks than outside the feeding patch when four or more basking sharks were observed feeding at the surface. When only a single individual was observed feeding at the surface, however, zooplankton abundance was not unusually great nor did single animals always feed on dense surface concentrations of copepods. Occasionally, single animals were feeding in an area with greater zooplankton density than in an area near the shark. This was the case on five occasions in British Columbia and two occasions in the Gulf of Maine. There also were a few occasions where zooplankton densities were greater away from a feeding individual than where it was feeding.

The observed feeding behavior of basking sharks may be related to these measurements of zooplankton abundance in each study area. In Monterey Bay and in the Santa Barbara Channel Islands, sharks were feeding at the surface persistently for several hours. I assumed these sharks were feeding because their mouths were agape. Generally, sharks were sighted at the surface in the morning hours until the wind increased and in the evenings when the wind receded (Darling and Keogh, 1994; personal observation). Basking sharks also

were observed feeding at the surface at night (personal observation, Captain Rick, Fort Bragg, pers. comm.). Basking sharks may follow the diel vertical migrations of their major prey item, copepods. When copepod surface densities were great, it is possible basking sharks remained in the area until zooplankton were depleted. During the feeding events in Monterey Bay in 1991, approximately 15 to 20 sharks were observed repeatedly and remained in the north bay area for one month.

In British Columbia, each individual usually was sighted at the surface for less than five minutes duration and then dove. Perhaps, these individuals were sampling surface water for prey abundance, or randomly surfacing without feeding. Feeding behavior (with mouth agape) was confirmed on one occasion in Clayoquot Sound. On the other occasions, the position of the mouth was too far underneath the water's surface for observation or the boat was unable to approach the animal closely before the animal dove. Possibly, the sharks sighted in British Columbia were not feeding when the samples were collected. All basking sharks observed in Monterey Bay were swimming with mouth agape. Basking sharks were observed feeding at the surface for several hours in Monterey Bay. Hallacher (1977) reported basking sharks swim with their mouth agape and periodically close it every 30 to 60 seconds to engulf prey. In Maine, however, individuals sampled during this study remained at the surface for a period of one half hour or more with mouths closed (S. Katona, A. Zoidis, and S. Martin, pers. comm.). Also, surface densities were greater outside the feeding area on two of four occasions in the Gulf of Maine. Possibly, when sharks feed at the surface, they can detect prey, and if prey density reaches a minimal level, the individual remains at the surface without feeding. Minimal densities observed

inside feeding areas in Maine were greater than minimal densities observed in Clayoquot Sound, but both were below the levels recorded in Monterey Bay or off the Santa Barbara Channel Islands.

The presence of the sampling vessel may have affected the feeding behavior of sharks at the surface. The effects of boats and other forms of disturbance on basking shark feeding behavior are unknown. Darling and Keogh (1994) photo-identified individuals, and described nicks and wounds on the dorsal fin. They suggested these cuts probably were caused by boat propellers. They also recorded that sharks were behaviorally attracted to their boat propeller. I have observed both indifferent behavior and evasion to boat presence by feeding basking sharks.

If basking sharks detect and recognize prey patches, they must possess sensory apparatus and capabilities for prey detection. First, the olfactory organ of basking sharks is similar to many smaller elasmobranchs (i.e.: *Scyliorhinus stellaris*), and may be specially adapted to ensure a continuous flow of water and chemical testing of the water (Matthews and Parker 1950). The nares are situated closely and slightly anterior to the mouth on each side of the head. They form two scoop-shaped funnels at the skin's surface, which allows a continuous water stream that enters the first funnel, passes through the olfactory organ, and exits by the second funnel when the fish swims forward.

The lateral line canals are not exceptionally developed along the body of basking sharks. The tubules of the antorbital region of the head, however, are more closely spaced and numerous and their openings are almost indistinguishable from the enormous number of ampullary openings. The most extensive group of ampullae of Lorenzini pits occur on the supraorbital region of

the head, with a maximum density of 60 to 80 per cm^2 (Matthews and Parker, 1950). The ampullae and their tubules are concentrated into a large mass which, along with the ampullae of the outer buccal region, occupies the whole space above the rostral cartilage (Matthews and Parker, 1950).

While these sensory apparati may provide capabilities for short range detection, there is no mechanism known for long range prey detection of copepod surface swarms. Owen's (1984) observations of basking shark sightings in New England waters and Choy and Adams (in prep.) observations in Florida waters may offer an explanation. Owen reported the seasonal occurrences of basking sharks were correlated positively with development of the thermocline. Sightings per unit effort (SPUE) were greatest during the summer when the thermocline was well developed. Sightings/unit effort declined up to two months before the decline of stratification. Additionally, sightings/unit effort were great between two thermal ridges, particularly along the shoreward slope of the outermost ridge in the area of possible convergence. It is possible that basking sharks use thermal fronts and convergence zones to locate prey concentrations over great distances as was observed with right whales in the Great South Channel (Wishner et al. 1988). Owen also reported that there were only occasional associations between sightings of basking sharks and oceanic fronts. Choy and Adams (in prep) observed a basking shark feeding at the surface for approximately 40 minutes along the warmer side of a thermal convergence line off Cape Canaveral, Florida.

Observations off Newfoundland, California, and New England indicated appearance of basking sharks at the surface was positively correlated with temperature. Lien and Fawcett (1986) found 90% of shark entanglements in

salmon nets and cod traps in Newfoundland occurred when surface temperatures were 8 to 12° C. Incidental captures rarely occurred until water temperatures were 6° C, and were not common until 8° C. Squire (1967) reported that basking sharks were least abundant in Monterey Bay when surface water was greater than 14° C. Off New England, basking sharks were sighted when temperatures ranged between 11 and 24° C (Owen 1984), and the greatest number of sightings occurred in summer when temperatures were between 16 and 24° C. The greatest concentration of sharks occurred in water temperatures of 22 to 24°C. Basking sharks may be attracted to waters of certain temperatures initially, and subsequently sharks may use thermal fronts as a cue to find prey because prey is often concentrated along convergence zones of different temperatures.

Although the range of many shark species may be related to water temperature (Castro 1983), the basking behavior of these sharks may not be regulated by such mechanisms. Other lamnid sharks such as *Isurus oxyrinchus*, *Carcharadon carcharias*, *Lamna nasus*, and *Lamna ditropis*, typically maintain deep red muscle temperatures 4 to 12° C above ambient water temperature and operate efficiently in pelagic cold-water environments (Carey et al. 1985). Carey et al. (1971) determined an average 1° C difference between surface water and muscle temperatures in five basking sharks. Basking sharks, like other lamnids, may maintain body temperature above ambient water temperature despite their low swimming speeds. Therefore, its distribution may not be regulated solely by water temperature. Because the basking shark is observed feeding at the surface in such a wide range of water temperatures, (8 to 24° C), the distribution of this species at the surface may not be related solely to temperature.

Basking sharks also may appear at the surface for reasons other than feeding. Perhaps the basking habit may be attributed to an orientation towards sunlight. Darling and Keogh (1994) noted that sharks were sighted more frequently on calm, sunny days. Although sighting effort was biased toward sunny days, most searches when sharks were absent occurred on overcast and/or windy days. Assuming sightability was similar for sunny and overcast days, calm and sunny waters may have provided "comfortable" conditions for basking behavior (Leggett 1977).

During summer, individuals found off the British Isles were observed engaging in courtship activity, and mating scars were found on captured individuals (Matthews 1950). Matthews related the basking habit to courtship and breeding behavior, however observations were inconclusive. This explanation was rejected by Maxwell (1952) and Watkins (1958) because many immature sharks were observed basking among the adults. Also, there is evidence that mainly females bask at the surface. In the Scottish fishery, whenever large numbers were observed, the sex ratio was never less than 10 females per male, however, the overall sex ratio of the Scottish fishery were not as great (Kunzlik 1988). Both Matthews (1950) and Owen (1984) observed groups of basking sharks swimming in large "head to tail" circular formations, and Matthews (1950) also associated this behavior with courtship. I observed this behavior on one occasion when five sharks were observed feeding at the surface in Monterey Bay.

It is not unusual that a filter-feeding predator like the basking shark feeds on such abundant prey items as *Calanus*. spp. Basking sharks are passive feeders, and probably do not select *Calanus* sp. Rather, *Calanus* sp. are

cosmopolitan, swarming copepods commonly found in very high densities (Marshall and Orr 1955). For this reason, the diet of basking sharks is composed mainly of this taxonomic group. Surface patches of *C. finmarchicus* are well known occurrences in spring and summer throughout much of its range, and have been termed "clouds", "red feed", or "cayenne" (Bigelow 1924, Marshall and Orr 1955, Wiborg 1976). Coincidentally, the same descriptions have been used to describe the red soupy gut contents of basking sharks (Matthews and Parker, 1950, Parker and Boesman 1954). Other calanoid copepods also form large surface or subsurface patches or dense layers in the open ocean, including *C. tonsus* in the subantarctic south of Australia (Kawamura 1974), *C. cristatus* (*Neocalanus cristatus*) across most of the subarctic Pacific (Barraclough et al. 1969), *C. pacificus* (this study), and *C. pacificus* copepodite stage V's at 450-m depth off California in autumn (Alldredge et al. 1984).

The significance of copepod swarming behavior in maintaining dense patches should be considered. Wishner et al. (1988) reported species-specific swarming behavior may be involved in *Calanus sp.* patch formation because *Calanus sp.* concentrations were much greater than other copepod species. Although *Calanus sp.* and non-*Calanus sp.* copepods were more concentrated in the patch than below the patch, *Calanus sp.* were approximately 20 times greater in density than other copepods. This indicates that *Calanus sp.* behavior, such as seasonal swarming, also was important in structuring and maintaining the patch (Wishner et al. 1988). Predator feeding behavior also may influence patch size, shape, and dimensions. Wishner et al. (1988) observed the outer edges of the patch marked with the presence of large numbers of exoskeletons and partially decomposed copepods. This may have resulted from intense predation by

feeding right whales.

The temporal distribution of basking sharks in surface waters also may be related to the occurrence of *Calanus sp.* in the diet. Basking sharks are typically sighted seasonally off North America during periods when their prey is known to swarm. Basking sharks may feed on calanoid copepods with greater frequency than other zooplankton taxa which swarm during other seasons of the year. In this manner, basking sharks may be temporally segregated from feeding on other surface prey items. Copepods constitute the main component of zooplankton biomass and production in many regions including the Antarctic (Boysen-Ennan et al. 1991), therefore, provide a valuable resource for large filter-feeding vertebrates.

It seems unusual that euphausiids and other swarming crustaceans are not abundant in the diet of basking sharks. Larval euphausiids and deep sea *Sergestes* were found in the stomach contents of basking sharks but adult euphausiids were uncommon in the diet (this study, Mutoh and Omori 1978). Although some baleen whales feed on copepods, most balaenopterids feed on swarming euphausiids or small schooling fishes (Leatherwood 1983). Balaenopterids are more active feeders than basking sharks and can catch these faster-swimming prey items. It is possible that basking sharks do not prey on euphausiids because they cannot maintain swimming speeds necessary to catch them.

Prey Energetics

Matthews (1962) calculated that an average sized basking shark needs an hourly intake of 663 kcal to sustain foraging activity, and as zooplankton abundance declined below this level in winter, sharks shed their gill rakers and

hibernated. Dry weight zooplankton estimates from this study were converted to a caloric equivalent based on an average caloric content of 5.8 kcal/g dry weight taken from Table 1 in Tremblay and Roff (1983). The resulting caloric content per m^3 was multiplied by 1484m^3/hr, the filtration rate of an average sized (7 m) basking shark (Parker and Boesman 1954). According to these equations, the greatest caloric values of available zooplankton calculated for each study area were 5174 kcal/hr for Monterey Bay, 4443 kcal/hr for the Santa Barbara Channel Islands, 799 kcal/hr for the Gulf of Maine, and 292 kcal/hr for British Columbia. Although these are very gross estimates of caloric value, only the British Columbia estimates fall below the requirements proposed by Matthews (1962).

Basking sharks are continuous ram feeders (Sanderson and Wassersug 1990) and expend great amounts of energy swimming with mouth wide open while filtering. In fact, it is possible the basking shark must balance an energy budget between spending more energy capturing prey than they can obtain from it. The energy expended due to drag when filtering is much greater than swimming with mouth closed. In order to save energy, basking sharks may filter feed only when zooplankton is abundant (Bone et al. 1995).

Food Habits

The taxa identified from nine stomach contents collected off St. John's, Newfoundland were similar to taxa determined from inside basking shark feeding areas off Monterey Bay, British Columbia, the Gulf of Maine, and Santa Barbara Channel Islands. Clearly, calanoid copepods, particularly *Calanus*, are important prey items for basking sharks.

Metridia longa, the most important prey item found in the nine stomach

contents, also, is a dominant oceanic copepod in shallow coastal waters (0-500 m) off Newfoundland (Alsuth 1989). Members of this genus are usually strong diel vertical migrators (Brodskii 1967, Geinrikh et al. 1983). Most *M. longa* individuals (>90%) found in the gut contents were adult females. *Metridia longa* females typically migrate into surface waters (0-100 m) from July-Oct (Geinrikh et al. 1983), the same season when basking sharks were entrapped in nets and stomach contents were collected. The repeated occurrence of *M. longa* females in the gut contents indicated basking sharks may have been subsurface feeding during daytime or surface feeding at night preceding entrapment in Newfoundland. If these sharks were feeding at the surface, it is unusual that *Metridia*, not *Calanus*, dominated six of nine stomach contents. *Metridia longa*, however, resides in the upper layers of the water column much longer than *Calanus sp.* (Geinrikh et al. 1983). It is difficult to interpret these results relative to basking shark feeding behavior due to the dirth of information regarding the diel vertical migrations and patch formations of *M. longa*. All gear which entrapped basking sharks was set in relatively shallow water (from surface to 10-30 m; Lien and Fawcett 1986).

Calanus hyperboreus and *C. finmarchicus* also were relatively important prey items found in the stomach contents, and adults from these oceanic species are associated with cold, deep water during summer months. Adult females and copepodites may rise to the surface during summer months. Adult females, CIV and CV copepodite stages of these two species, were identified from the gut contents. It is highly probable that these prey items were ingested by the basking sharks in surface waters.

In conclusion, many questions remain about the feeding ecology of basking sharks. Details regarding patch formation, patch distribution and integrity, and minimum density requirements for basking sharks feeding at the surface should be addressed. Basking shark feeding behavior and mechanisms for prey search and detection are poorly understood. Also, energetic requirements have not been completely resolved and the effects of basking shark predation on copepod communities have not been addressed. Lastly, we are continuously mystified by the seasonal basking habit and subsequent disappearance of these predators from surface waters. When we can observe and continuously follow basking sharks in their natural environment for long time periods, we may be able to successfully unravel the complex and variable interactions between this predator, its prey, and the environment.

Chapter 2

Distribution and Abundance of Zooplankton Relative to Basking Shark Sightings in Monterey Bay, California

INTRODUCTION

Many aspects of the biology, life history, and ecology of basking sharks are still speculative. These include the distribution of the basking shark during winter (Matthews 1950, Parker and Boeseman 1954), the hypothesis regarding gill raker shedding in response to seasonal declines of zooplankton (Parker and Boeseman 1954, Matthews 1962), age and growth determination and verification (Parker and Stott 1965, Stott 1982), regional abundance estimates (Parker and Stott 1965, Squire 1967, Owen 1984, Horsman 1987, Squire 1991), and seasonal migration patterns (Matthews 1950, Parker and Stott 1965, Stott 1984, Owen 1984, Lien and Fawcett 1986).

Seasonal appearance of basking sharks at the surface and subsequent disappearance is believed to be the result of vertical and/or horizontal migration (Compagno 1984, Owen 1984). Along the Atlantic coast of North America, basking sharks appear in the southern part of their range in spring (North Carolina to New York), shift northward in summer (New England to Nova Scotia), and disappear from observation in autumn and winter (Kenney et al. 1985, Owen 1984, Lien and Fawcett 1986). Along the eastern North Pacific, basking sharks occur in greatest number during autumn and winter in the southern range (California) and shift northward in spring and summer (Washington and British Columbia; Squire 1967, 1991). A similar trend occurs off the British Isles, with peak abundance during summer and lesser numbers by autumn (Kunzlik 1988).

Matthews (1950) and Nikolsky (1963) speculated that basking sharks move into coastal shallow waters from deeper waters during the spring and summer to feed on zooplankton, mate, and return to deeper offshore waters in autumn. Parker and Stott (1965) suggested movements occur along a northerly gradient in spring and summer followed by a southerly movement during autumn. Few observations exist which support these hypotheses.

Off California, basking sharks have been observed from October to May, with greater concentrations occurring off Pismo Beach and in Monterey Bay (Squire 1991). In Monterey Bay, an average density of 42.1 basking sharks per sighting in one block area (148 km^2) was reported during aerial surveys conducted by fish spotters (Squire 1991). Peak abundance occurred in October, with fewer animals sighted in February and March (Squire 1967, 1991). Most recently, 78 basking sharks were marked with Floy tags during December 1990, and December 1991 in Monterey Bay (Sean VanSommeran, Pelagic Shark Research Foundation, pers. comm.). Six of the 38 sharks tagged in 1990 were resighted in Monterey Bay in December, 1991. This high resight rate supports the idea that local populations move into surface waters seasonally.

Although there is extensive information about seasonal cycles of phytoplankton abundance in Monterey Bay (Bolin and Abbott 1963, Silver and Davoll 1976, Waidelich 1976, Garrison 1976, 1979, Schrader 1981), virtually no information has been collected regarding the seasonal cycles of zooplankton there. Silver and Davoll (1976, 1977) and Waidelich (1976) conducted net tows for zooplankton during their phytoplankton surveys (Fig. 18), but only displacement volume (ml/1000m^3) was recorded and few zooplankton samples were collected. Displacement volumes may be a poor indicator of abundance if

large volumous invertebrates such as coelenterates are present in the sample (Omori and Ikeda 1984). These displace a much greater water volume than smaller organisms such as copepods, therefore, resulting in overestimates of abundance. It was difficult to determine seasonality or spatial differences using the information reported in Silver and Davoll's report (Fig. 1). For these reasons, I initiated zooplankton surveys in Monterey Bay from November 1991 to August 1993.

Monterey Bay spans approximately 44.3 km and is exposed to the open ocean and California Current System (Fig. 19). The most prominent bathymetric feature of Monterey Bay is the submarine canyon that begins approximately 100 m offshore Moss Landing Harbor and reaches approximately 1830 m depth. Hydrographic seasons have been described for the area (Skogsberg 1936) and confirmed by subsequent research (Bolin and Abbott 1963, Abbott and Albee 1967, Smethie 1973). These seasons include an upwelling season from February to September, an oceanic period September through October, and the Davidson current period from November to February.

Coastal upwelling is driven by persistent northwest winds that characterize spring and early summer months. The length of the upwelling season varies annually, and upwelling events may be sporadic at the end of the season. Upwelling also may occur after any period of persistent northwest winds (Smethie 1973). For example, Smethie (1973) documented an unseasonal upwelling event during the Davidson period in December 1971. With the relaxation of upwelling, the oceanic period is characterized by onshore flow of offshore waters. Oceanic periods are not always well marked (Bolin and Abbott 1963) and may be obscured by sporadic upwelling after the end of the upwelling

season. During the Davidson current period, the California Countercurrent surfaces between the coast and the California Current system and flows north. This results in onshore water flow, downwelling, and deep mixing along the coast (Smethie 1973).

Phytoplankton cycles generally follow a similar seasonal pattern with low winter levels, due to low light levels in winter and a well mixed water column, a spring bloom associated with increasing light levels and enhanced nutrient concentrations, and an autumn bloom which results from the relaxation of zooplankton grazing pressure (Waidelich 1976). Zooplankton abundance follows a similar pattern related to the hydrographic seasons but is not as well marked (Fig. 18; Silver and Davoll 1976, 1977, Waidelich 1976). The zooplankton maximum appeared one month before the phytoplankton maximum during the spring bloom (Waidelich 1976). This observation is different than those among other mid-latitude marine ecosystems in which the zooplankton bloom lags approximately one month behind the phytoplankton bloom. Waidelich (1976) attributed this discrepancy to sampling error. Similar to the annual phytoplankton cycle, there appears to be a spring and autumn zooplankton bloom (Fig. 18).

The main objective of this portion of the study was to determine if there was a relationship between the distribution and abundance of basking sharks and their zooplankton prey in the Monterey Bay. According to observations made by other authors, seasonal and spatial distribution and abundance of basking sharks should be positively correlated with seasonal distribution and abundance of zooplankton in Monterey Bay if basking sharks move into surface waters to feed.

METHODS

Basking shark distribution and abundance

Three aerial surveys were conducted for basking sharks from Pt. Lobos State Reserve to Año Nuevo Island. Two strip transects, approximately 200 m wide and 2 km offshore , were flown parallel to shoreline at approximately 305 m altitude. Additionally, vessel surveys for basking sharks were conducted between zooplankton sampling stations. These surveys covered ~10% of the total study area. Letters of request for opportunistic sightings were circulated among recreational and commercial boaters and pilots in the Monterey Bay area, and research institutions, state beaches, county parks, and marine reserves. Approximate location and number of individuals sighted were requested. Additionally, historical records were compiled from 1948 to 1951 from the flight logs of an aerial fish spotter, Edward Durden. Durden's systematic flights covered three block areas (approximately 14.9 x 18.6 km each) of Monterey Bay. Opportunistic historical sightings also were obtained and compiled from Alan Baldridge, Hopkins Marine Station, Stanford University, and Robert Lea, California Department of Fish and Game.

Historical sighting records and sightings reported during this study were compared by graphing mean monthly basking shark sightings for each observation period.

Zooplankton distribution and abundance

Zooplankton surveys were conducted in Monterey Bay from November 1991 to August 1993. Zooplankton were sampled at least two times per season using a 335 μm, 0.5 m diameter, 3-m length Puget Sound opening/closing plankton net (Research Nets). A pre-calibrated flow meter (General Oceanics

Model #2030) was mounted at the mouth of the net to reliably estimate water volume filtered per tow. On five occasions when a flow meter was unavailable for use, length of wire deployed and wire angle were used to calculate volume of water filtered per tow. Six regions of Monterey Bay were sampled each cruise: A) nearshore north bay, B) nearshore central bay, C) nearshore south bay, D) offshore south bay, E) offshore central bay, and F) offshore north bay (Fig. 19). One station was sampled per region (six stations total) on each survey day. Three sets of stations were chosen randomly and sampled throughout the study period, Sets A, B, and C (Table 11). The offshore central station in Set A was deliberately chosen because it had been sampled historically in Monterey Bay (Bolin and Abbott 1963). To study temporal variability in zooplankton abundance, six fixed stations were sampled every other survey throughout the study period (Set A stations). Six alternate stations were sampled one to two times per season in 1991/1992 (Set B stations) and one to two times per season in 1992/1993 (Set C stations). The additional sets (Sets B and C) were added to increase the area sampled to determine spatial variability in zooplankton abundance. Because each survey event sampled a different water column at the same station than the previous survey, each sample was treated as a random sample (Cassie 1968).

Vertical zooplankton tows were collected as representative samples of seasonal abundance of zooplankton in the upper 100 m of the water column. Due to great variability reported for surface concentrations of zooplankton (Cassie 1959, 1968), surface tows were not collected as representative samples of seasonal zooplankton abundance. Two replicate vertical tows per station were conducted from 100 m depth to the surface in 1991/1992. Vertical tows were

sampled from the bottom to surface at stations with shallow depths (20-60 m) in 1991/1992. To standardize tow depths, vertical tows were collected from 50-m depth to the surface at all stations in 1992/1993.

All zooplankton samples were preserved in approximately 10% buffered formalin in sea water (Salonen and Sarvala 1985). All large cnidarians were removed from samples. Samples were sub-sampled using a Stempel pipette, filtered and rinsed with deionized water, and dried in an oven (Blue M) at 60 +/- 10 ^{o}C (Omori and Ikeda 1984) for at least 48 hrs. Next, samples were weighed to the nearest 0.001 gram using an electronic balance. Subsample weight was multiplied by the dilution factor of the total sample to determine total weight of the sample. Biomass was quantified by dividing dry weight by volume of water filtered (mg/m^3).

A four-factor Analysis of Variance (ANOVA) was used to determine the differences in mean zooplankton biomass among years, seasons, regions, and sites (Zar 1984, Underwood 1981, Systat 1992). Samples were divided into November 1991 through September 1992 and October 1992 through August 1993 for annual categories. Seasons were divided into three oceanographic seasons, upwelling (February to August), oceanic (September to November), and Davidson (December to February; Skogsberg 1936, Bolin and Abbott 1963, Abbott and Albee 1967, and Smethie 1973). Regions were divided into north (north of 36^{o}50'N latitude), central (between 36^{o}50'N and 36^{o}45' N latitude), and south (south of 36^{o}45'N latitude), and sites were divided into nearshore (east of 121^{o} 55' W latitude) and offshore (west of 121^{o} 55' W latitude and greater than 100 m depth; Fig. 19). A Bonferroni multiple comparison test was used to determine the differences among significantly different levels of ANOVA factors

(Day and Quinn 1989). Also, a more conservative alpha error (a=0.01) was employed on a posteriori t-tests performed in series on the year*site interaction term.

Relationship between basking shark and zooplankton distribution and abundance

The relationship between shark and zooplankton distribution and abundance was compared by graphing monthly mean sightings of basking sharks and monthly mean zooplankton biomass estimates for November 1991 through August 1993. Historical records of basking sharks were not used for the comparison because historical observations differed temporally with zooplankton surveys conducted during this study.

The relationship between basking shark and zooplankton distribution and abundance among the seasonal, regional, and site factors of the ANOVA were compared graphically. Mean abundance of basking shark sightings and maximum group size were plotted with mean zooplankton abundance for each season, region, and site throughout the study period.

Assessment of sampling and experimental design

Several projects were conducted to assess the power of the sampling and experimental design of this study. Ten replicate zooplankton tows were collected at one central nearshore station on 31 March 1992 to determine optimal replicate size. Precision (measured as standard error/mean) versus sample size was plotted along with cost per unit sample. Cost was measured as time required to complete an additional tow. Optimal replicate size was determined by calculating where the product of cost and standard error/mean was least.

Similarly, ten random samples were collected in one of the six study regions (central nearshore) on 31 March 1992 to assess regional variability in zooplankton biomass and to determine an optimal sample size per region. Precision and cost versus sample size was graphed to determine the optimal number of stations per region. The variability among stations in the central nearshore region was calculated to determine minimum detectable effect size of the regional replicate size allocated for this study.

Dry weight also was evaluated for its utility as a reliable indicator of zooplankton biomass. Number of individuals/m^3 water volume filtered were enumerated and correlated with dry weight estimates from ten tows sampled from Monterey Bay. Spearman rank correlation was used to determine the reliability of dry weight as an estimate of actual numbers of individuals counted.

RESULTS

Basking shark distribution and abundance

No basking sharks were observed during the aerial surveys from Point Lobos State Reserve to Año Nuevo Island, and none were sighted during zooplankton surveys. Only 17 basking shark sightings were reported in the Monterey Bay area from November 1991 to August 1993 (Fig. 20). Most sightings occurred in May (n=3), August (n=7), and December (n=4; Fig. 21). The largest group size observed was 30 sharks on 08 August 1992 directly off the kelp bed at Big Creek, Big Sur. Also, a concentration of approximately 15 to 20 basking sharks (40 total individuals were tagged) was observed repeatedly off Long Marine Lab, Santa Cruz, during November and December 1991. All reported sightings were opportunistic and no measure of effort was calculated.

Excluding February, the observations recorded from 1967 to 1994 (A. Baldridge and R. Lea, unpubl. data) were similar to the observations recorded in this study, with three peaks in average shark abundance in January, August, and November. From 1948 to 1951 (Durden's aerial censuses), peak abundance occurred in March and October. Overall, current basking shark abundance appears less in Monterey Bay than historical abundance.

Zooplankton distribution and abundance

Seventeen zooplankton surveys were conducted from 11 November 1991 to 17 August 1993. An average of three random surveys per season were conducted (Table 12). Zooplankton abundance was greatest in February, May, and August-October (Table 13; Fig. 23).

Mean zooplankton biomass was significantly different among seasons ($F=3.64$, $n=191$, $p=0.029$) but was not related to year, region, or site (Table 14). Mean zooplankton abundance was greater significantly during the oceanic season (Sept-Nov) compared with the Davidson season (Dec-Feb; $d=15.37$, $n=151$, $p=0.026$; Fig. 24). There were no significant differences between the upwelling (Mar-Aug) and Davidson seasons or between the upwelling and oceanic seasons (Fig. 24). Also, there was a significant interaction in mean zooplankton biomass between years (1991/1992 and 1992/1993) and sites (nearshore and offshore). In 1991/1992, mean zooplankton biomass was greater (>10 mg/m^3) nearshore than offshore. In 1992/1993, mean zooplankton biomass was greater (approximately 2 mg/m^3) offshore than nearshore. Mean zooplankton abundance nearshore was significantly greater than offshore in 1991/1992 ($t_{one\text{-}tailed}=2.15$, $n=40$, $p=0.035$) but not in 1992/1993 ($t_{one\text{-}tailed}=-0.40$, $n=40$, $p=0.69$; Fig. 25).

Relationship between basking shark and zooplankton distribution and abundance

There were three general corresponding peaks in basking shark and mean zooplankton abundance in May, August, and November (Fig. 23). There were no apparent seasonal relationships between maximum group size of basking sharks sighted per day or mean basking shark abundance and mean zooplankton abundance. Groups of basking sharks, however, were observed feeding in dense copepod patches during the oceanic season of 1991 (Fig. 24). Mean number of basking sharks and mean zooplankton abundance was greater nearshore than offshore in 1991/1992. The greatest mean abundance of sharks and zooplankton occurred in the north bay (Fig. 26), however, there was no statistical relationship.

Sampling and Experimental Design

Precision increased and stabilized after five replicate tows were sampled at a central nearshore station in Monterey Bay (Fig. 27). Cost (time/unit tow) increased linearly with increasing sample size. Optimal replicate size (where product of cost and precision (SE/mean) was least) was three replicates per station. Only two replicates were conducted per station in this study.

Precision fluctuated and decreased continually for all ten net tows collected among different regional stations (Fig. 28). Cost increased linearly with increasing sample size per region. Optimal sample size per region was two stations per region.

Assuming the variability of one region (i.e. central nearshore) was representative of all six regions sampled in this study, 3.3 samples per region were required to detect a doubling in zooplankton biomass. Three samples per region effectively detected a 2.6 biomass increase.

There was a significant positive correlation between number of individuals enumerated and dry weight measurements (r_S=0.939, n=10, p<0.001; Fig. 29). Dry weight measurements, therefore, were a reliable estimate of zooplankton abundance.

DISCUSSION

Sampling and Experimental Design

The greatest limitation in the sampling regime for this portion of the project was the method in which shark sightings were obtained. All sightings of basking sharks were opportunistic, and sighting effort was not recorded. Effort could have been measured for the three aerial surveys and zooplankton boat surveys, but no sharks were sighted on any of those surveys. Consequently, one can assume that with great effort, only a few basking sharks may have been seen, and overall shark abundance at the surface was low in Monterey Bay from November 1991 to August 1993. The number of vessels operating and/or the number of observers on land may have biased the sighting rate and frequency. The great number of sharks and more frequent sightings of sharks in summer months (i.e. July and August) may be related to the greater number of observers on the water and/or on land during these months. All sightings were confirmed and species identity was verified. The daily coverage of the bay by recreational and commercial boaters is quite high. Monterey Bay has many prey resources that attract a large number of commercial and recreational boaters from four ports at Santa Cruz, Capitola, Moss Landing, and Monterey. Additionally, there are five research institutions with vessels that travel and sample throughout Monterey Bay area regularly throughout the year. Although single individuals

may have been missed, I assumed that most groups of basking sharks feeding at the surface would have been sighted and reported. Another potential problem regarding basking shark abundance was that presence of sharks could have been detected only when sharks were swimming at the surface. Basking sharks which may have been present in deeper waters would not have been detected by observers at the surface.

Design of the zooplankton surveys was assessed and only three stations per region were sampled during the two year duration of the study to determine the spatial differences in zooplankton abundance. Eighteen total stations were sampled to represent the spatial distribution of zooplankton abundance in the 550 km^2 area of Monterey Bay. The spatial area sampled, therefore, was greatly limited and probably does not describe completely the spatial distribution of zooplankton in Monterey Bay. The low precision determined for the central nearshore region of Monterey Bay also indicates that spatial coverage was greatly limited. The precision curve never stabilized when ten random zooplankton tows were conducted in a 74 km^2 area. This sampling scheme, however, adequately revealed large scale spatial differences in zooplankton abundance (i.e. the greater nearshore mean zooplankton abundance measured in 1991/1992). Two to three surveys per season were conducted for the duration of the study to determine temporal differences in zooplankton abundance. The temporal sampling regime also was greatly limited and probably does not describe completely the temporal distribution of zooplankton in Monterey Bay. This temporal sampling regime, however, revealed large scale temporal differences in zooplankton abundance (i.e. The oceanic season (Sept-Nov) was significantly greater in mean zooplankton abundance than the Davidson season

(Dec-Feb). Additionally, dry weight (mg/m^3) was used as an indicator of zooplankton abundance. Although this indicator was a more gross estimate of zooplankton abundance than enumeration, it was a reliable estimator for measuring large scale differences in zooplankton abundance.

Basking shark movements, distribution and abundance

Abundance of basking sharks from 1967 to 1994 and from November 1991 to August 1993 was much less than the abundance of sharks observed by the aerial fish spotters from 1948 to 1951. This decrease may be related to overfishing. Basking sharks were the subject of a small commercial fishery in Monterey Bay in the 1940's. The sharks were captured for liver oil and for reduction into fish meal (Phillips 1948). During September 1946 to May 1947, approximately 300 basking sharks were taken between Monterey Bay and Morro Bay, California (Phillips 1948). Due to low prices paid for shark liver oil, and a decline in the availability of sharks, fishing was suspended in October, 1950. Slow growth rates and low reproductive rates (Parker and Stott 1965, Stott 1984), probably, have kept basking sharks from recovering from these activities.

Because sighting effort was not measured, the temporal and spatial distribution and abundance of basking sharks in Monterey Bay could not be statistically verified. However, trends may still be observed from opportunistic sightings. The possibility of seasonality in basking shark distribution and abundance in Monterey Bay remains unclear. Before this study, groups of sharks were sighted commonly from October to May in Monterey Bay (Squire 1967, 1991). In this study, groups of sharks were sighted in July and August, and sighting reports occurred throughout the year. The data compiled by Baldridge and Lea also indicated that basking sharks were sighted often in summer

months. Additionally, from 29 July to mid-August 1976, great numbers (>50) of basking sharks repeatedly were observed feeding in Carmel Bay (Hallacher, 1977). Groups of basking sharks (up to 20 individuals) were also sighted in July and August, 1992, 1993, and 1994, just outside the kelp line off Big Creek Reserve, Big Sur, California. The seasonality of basking sharks is not well marked and basking sharks can be sighted during any time of the year.

Owen (1984) concluded from seasonal changes in density of basking sharks (1979-1980), distance from continental shelf edge, and water depth at sighting, that basking sharks completed an offshore-inshore movement from spring to summer in New England waters. During spring, seasonal densities were greatest in partially stratified deep, offshore waters (median depth=86 m) along the southern and eastern slopes near Georges Bank. In summer, density of basking sharks increased dramatically in nearshore waters (median depth=68 m) of the Gulf of Maine and southern New England waters. This increase in density of sharks nearshore corresponded with a similar decrease in densities of basking sharks in the Georges Bank region. During autumn, sightings decreased to spring levels in the Gulf of Maine whereas the average density around Georges Bank remained unchanged. There were no sightings in southern New England waters in autumn and during winter in any of the three regions.

From catches of basking sharks in the Norwegian fishery from 1971-1973, Stott (1982) reported there was an inshore migration off the western coast of Norway in May. Sharks were captured along the entire coastline of Norway in June and July from 1971-1973. In all three years, sharks were captured at the end of the season in September, mostly off the northwest coast of Norway. Incidental catches of basking sharks off Newfoundland (1980-1983) occurred initially and

most commonly in May on the southwest coast of Newfoundland. Incidental catches on the northeast coast also were common but were more scattered and occurred later in summer in September. Occasional winter catches by trawlers fishing in the deep waters of the Gulf of Saint Lawrence indicated that some basking sharks occurred there during winter (Lien and Aldrich 1982).

Although it is apparent that there is an onshore seasonal movement of basking sharks towards nearshore waters, no complete migration route has been documented. There appear to be no consistent movements within or among years. Published records indicated great variability in basking shark abundance over periods of years (Bigelow et al. 1948). These records represent the scarcity of basking sharks off the Norwegian coast during the first half of the 18th century and the middle of the 19th century which alternated with periods of greater abundance in 1800 and 1880.

Distribution and abundance of zooplankton

The seasonal trends in zooplankton abundance observed during this study were representative of similar trends observed for the phytoplankton cycle in Monterey Bay, with a spring and autumn bloom and decreased abundance in winter months. Although the greatest zooplankton biomass observed in May was greater than any measurement observed during the oceanic season, the mean biomass was statistically greater in the oceanic, not the upwelling hydrographic season, as one might expect. The peak in zooplankton abundance during upwelling, however, was brief and lasted approximately one month (May), and the biomass peak during the oceanic season was of greater duration, approximately three months (September through November). Additionally, the upwelling season had the greatest duration (six months) of all oceanographic

seasons. Therefore, the mean zooplankton biomass for the entire upwelling season also included months of reduced biomass levels such as March and July. Because of this variability, possibly, there were no significant differences in mean zooplankton abundance between the upwelling and Davidson seasons.

The low zooplankton levels recorded in Monterey Bay during February, March, and April 1992 and 1993 were probably related to the occurrence of an El Niño Southern Oscillation warm water event (ENSO) in 1991-1993. Water temperatures were 1-4^{o}C greater near the surface in May-June 1992, compared with the mean for May-June 1987-1992 (Sakuma et al. 1994a). Salinities, generally, were 0-0.8 ppt less near the surface. Movement of California Current water inshore towards the coast was the most likely explanation for the hydrography in 1992. Conditions during February to March 1993 off central California were characterized as a continuation of the ENSO that developed in early 1992 (Sakuma et al. 1994b). Temperatures throughout the water column (to 500 m) were cooler than for a similar period in 1992 (Sakuma et al. 1994b), but remained substantially warmer than the region's long-term average of the CalCOFI database. Temperatures were 1 to 3^{o}C greater than the mean for 1983-1993. The distribution of surface salinities and temperatures in May-June 1993 indicated there was an onshore displacement of California Current water similar to that seen in 1992 (Sakuma et al. 1994b). There was a large increase in zooplankton biomass from April 1992 to May 1992. This may have been the period when the dampening El Niño effects were overcome by a pulsed upwelling event in the bay. However, there were no significant annual differences in zooplankton biomass between upwelling events in 1991/1992 and 1992/1993.

Relationship between basking shark and zooplankton distribution and abundance

The strongest relationship between basking shark and zooplankton distribution and abundance occurred from November to December 1991 when at least 40 basking sharks were sighted feeding at the surface repeatedly off Santa Cruz. The data presented in Chapter 1 of this study demonstrated the association between schools of basking sharks and dense copepod patches. Clearly, zooplankton abundance was greatest throughout the bay during these months of 1991/1992.

There appears to be another strong relationship between basking shark abundance and zooplankton abundance nearshore and offshore in Monterey Bay. Zooplankton abundance, generally, is greater in nearshore than offshore waters of the California Current area (Reid et al. 1958, Colebrook 1977, Bernal 1980, Loeb et al. 1983), as observed during 1991/1992 of this study. Accordingly, basking sharks are typically sighted in nearshore surface waters, presumably feeding on abundant zooplankton. Surface feeding basking sharks were observed in offshore waters rarely, possibly because most of the population may be feeding at depth in the deep scattering layer or sighting effort is less offshore.

Because the movement patterns of basking sharks are somewhat unpredictable and have not been well documented, it has been additionally difficult to understand the purpose of these seasonal movements into nearshore surface waters. To determine whether basking shark movements were seasonally correlated with distribution and abundance of their prey, long-term tracking capabilities would be required to follow individual basking sharks over several seasons of a few years. Also, corresponding zooplankton abundance

should be measured at different levels in the water column; alongside, below, and above the feeding shark. Zooplankton abundance would be greatest in the vicinity of the shark if the shark follows and pursues the diel vertical migrations of its zooplankton prey. Priede (1984) tracked a basking shark with an attached UHF radio transmitter for 17 days in the Firth of Clyde, Scotland, using the ARGOS satellite data collection and location system. The shark remained in the Clyde Sea area for the duration of the track, foraged in a warm water mass along a thermal front which circulated near Ailsa Craig Island, and surfaced several times throughout the track. No depth information was collected. Monitoring ended prematurely when the tow line failed. A similar long term tag, coupled with depth measurement capabilities, could be used to determine the seasonal movements of basking sharks.

Many aspects about the life history of the basking shark remain unknown. Fundamental information about its distribution and abundance in nearshore waters and subsequent disappearance is scant. Distribution and movements probably are related to prey abundance and reproduction. A more rigorous examination of the relationship between the distribution and movements of basking sharks and their prey is required to understand more clearly the ecology of this species in its natural environment.

CONCLUSIONS

Basking sharks feed in surface waters of great zooplankton abundance. The minimum number of sharks sighted feeding at the surface was positively correlated with mean zooplankton abundance. Groups (4-20 individuals) of basking sharks fed on dense copepod aggregations in Monterey Bay and off the Santa Barbara Channel Islands. Zooplankton density in feeding areas of basking sharks was significantly greater (6 to 42 times greater) than away from feeding areas in Monterey Bay and Santa Barbara Channel Islands. Although it has been suspected that basking sharks seasonally migrate into nearshore surface waters to feed in areas of high zooplankton abundance, these are the first measurements of basking sharks feeding in areas of great copepod density. In Clayoquot Sound, B.C. and the Gulf of Maine, basking sharks were sighted swimming individually at the surface with no association to dense swarms of copepods.

Calanoid copepods, especially *Calanus spp.*, are important prey items in the diet of basking sharks. *Calanus pacificus* was the most important prey item in Monterey Bay, British Columbia, and off the Santa Barbara Channel Islands and was more important near feeding areas than away from feeding areas. Similarly, *Calanus finmarchicus* was the most important taxon found in basking shark feeding areas in the Gulf of Maine and was more important near feeding areas than away from feeding areas. *Metridia longa, Calanus hyperboreus,* and *C. finmarchicus* were the most important prey items identified from nine basking shark stomach contents collected off Saint John's, Newfoundland.

There may be an onshore seasonal movement of basking sharks to nearshore waters. However, there are no consistent movements within years or among years, and sightings of basking sharks can be sporadic. Basking sharks

may be sighted during any month of the year. The greatest frequency of shark sightings occurred in May, August, and November from November 1991-August 1993. The largest groups of basking sharks observed occurred off Santa Cruz (n-40 total) during November-December 1991, and Big Creek, Big Sur (n=30) in August 1992. Basking sharks were sighted throughout the year during this study. There were two annual peaks in zooplankton abundance in Monterey Bay from November 1991-August 1992, in autumn and spring. Zooplankton abundance was significantly greater during the oceanic than the Davidson current season. There were no significant differences in zooplankton abundance between the upwelling and Davidson season, or the upwelling and oceanic season. Zooplankton abundance was greater nearshore than offshore during 1991/1992, but not during 1992/1993. There were three corresponding peaks of basking shark and zooplankton abundances in May, August, and November. Both shark and zooplankton abundance were greater nearshore than offshore in 1991/1992 and during November 1991 in the north nearshore region when groups of basking sharks fed in areas of high zooplankton abundance.

Groups of basking sharks may migrate seasonally into nearshore surface waters to feed on abundant swarms of copepods. However, basking sharks sighted feeding at the surface during other times of the year may be responding to periodic increased levels of zooplankton abundance. Individual sharks sighted swimming at the surface may not be associated with dense swarms of zooplankton. Therefore, basking sharks may move into surface waters for feeding and possibly for other purposes such as courtship and mating.

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Table 1: Taxa identified from zooplankton tows collected in basking shark feeding areas in Monterey Bay, British Columbia, Gulf of Maine, the Santa Barbara Channel Islands, and from basking shark stomach contents.

Taxon	Monterey Bay	British Columbia	Gulf of Maine	Santa Barbara Channel Islands	Basking Shark Gut Contents
Crustaceans					
Copepods					
Acartia clausii	X				
Acartia tonsa	X				
Acartia hudsonica		X			
Acartia longiremis		X			
Acartia sp.	X	X	X		
Calanus finmarchicus			X		X
Calanus glacialis					X
Calanus hyperboreus					X
Calanus pacificus	X	X		X*	
Centropages abdominalis		X			
Centropages bradyi	X				
Centropages hamatus			X		
Centropages typicus			X		
Corycaeus		X			
Ctenocalanus	X	X			
Cyclopoid	X				
Epilabidocera		X			
Eucalanus	X	X			
Euchaeta sp.					X
Haloptilus					X
Harpacticoid		X			
Labidocera	X				
Metridia longa					X
Metridia sp.					X
Oithona	X	X			
Paracalanus parvus		X			
Pontella meadii			X		
Pseudocalanus		X			
Rhincalanus	X				
Tortanus	X				
Unknown copepod		X			
Brachyuran zoea	X	X	X		
Crancridae	X	X			
Grapsidae		X			
Majidae	X	X			
Pinnotheridae	X	X			
Xanthidae		X			
Anomuran zoea					
Porcellanidae					
Pachycheles		X			
Petrolisthes		X			
Paguridae		X			
Caridea Hippolytidae		X			
Caridea Crangonidae		X			
Caridea Pandalidae		X			
Macrura Callianassidae		X			

Table 1 (continued): Taxa identified from zooplankton tows collected in basking shark feeding areas in Monterey Bay, British Columbia, Gulf of Maine, the Santa Barbara Channel Islands and from basking shark stomach contents.

Taxon	Monterey Bay	British Columbia	Gulf of Maine	Santa Barbara Channel Islands	Basking Shark Gut Contents
Megalopa larvae	X		X		X
Decapod larvae	X	X			X
Nauplii	X	X	X		
Cirripeds					
cirriped larvae	X	X	X		
cirriped legs		X			
Ostracods		X	X		
Amphipods	X	X	X		X
Hyperiid amphipod	X				
Isopods		X			
Euphausiids	X	X	X		X
Euphausia pacifica	X	X			
Megatyphines norvegica			X		
Nyctiphanes simplex	X				
Thysaenoessa spinifera	X	X			
Thysaenoessa gregani	X				
Coelenterates					
Salp	X				
medusae	X	X	X		
hydromedusae		X			
Ctenophores	X	X	X		
Chaetognaths	X	X	X		
Annelids					
Polychaete larvae	X	X			
Molluscan larvae	X	X	X		
Urochordates					
Oikopleura	X	X	X		
Teleosts					
Fish eggs		X			
Anchovy fish eggs	X	X			
larval fish		X	X		
Other				X	

X* Only *Calanus pacificus* copepods were identified from tows collected off the Santa Barbara Channel Islands.

Table 2: Modified Index of Relative Importance (MIRI), average and standard error values calculated for number (N), percent number (%N), and frequency of occurrence (%FO) of individuals for the ten most important zooplankton taxa found in zooplankton tows collected inside and outside basking shark feeding areas in Monterey Bay, California. n=number of tows collected inside and outside feeding areas.

	INSIDE TOWS (n=6)				OUTSIDE TOWS (n=12)			
Taxon	N	%N	%FO	Modified IRI	N	%N	%FO	Modified IRI
Calanus pacificus								
Average	901	78	100	7804	93	39	100	3883
Std.Error	352	9			39	8		
Acartia tonsa								
Average	17	2	100	215	23	36	100	3637
Std.Error	5	1			5	9		
Labidocera								
Average	2	0	50	5	3	2	92	192
Std.Error	1	0			1	1		
Tortanus								
Average	3	0	50	19	1	1	50	51
Std.Error	1	0			0	0		
Brachyuran zoea								
Average	13	3	50	169	2	1	42	27
Std.Error	10	3			1	0		
Euphausia pacifica								
Average	54	6	83	486	25	8	92	764
Std.Error	23	3			13	3		
Nyctiphanes simplex								
Average	11	3	33	107	0	0	25	2
Std.Error	11	3			0	0		
Chaetognaths								
Average	27	3	83	235	3	2	83	193
Std.Error	10	1			1	1		
Oikopleura								
Average	0	0	17	2	1	1	67	86
Std.Error	0	0			0	1		
Fish Eggs								
Average	4	0	33	15	7	5	58	318
Std.Error	3	0			4	2		

Table 3: Modified Index of Relative Importance (MIRI), average and standard error values calculated for number (N), percent number (%N), and frequency of occurrence (%FO) of individuals for the ten most important zooplankton taxa found in zooplankton tows collected inside and outside basking shark feeding areas in Clayoquot Sound, British Columbia. n=number of tows collected inside and outside feeding areas.

	INSIDE TOWS (n=24)				OUTSIDE TOWS (n=32)			
Taxon	N	%N	%FO	Modified IRI	N	%N	%FO	Modified IRI
Calanus pacificus								
Average	74	28	100	2817	93	19	94	1805
Std.Error	23	5			53	7		
Acartia sp.								
Average	19	13	100	1327	17	13	100	1250
Std.Error	4	3			4	3		
Centropages abdominis								
Average	23	10	96	946	21	15	97	1467
Std.Error	8	3			6	3		
Majidae zoea								
Average	2	1	76	49	0	0	50	17
Std.Error	0	0			0	0		
Brachyuran zoea								
Average	36	1	36	548	6	1	28	446
Std.Error	20	0			1	0		
Nauplii								
Average	7	2	68	122	7	5	78	365
Std.Error	2	0			3	2		
Ostracod								
Average	1	1	56	42	4	3	69	183
Std.Error	0	0			1	1		
Hydromedusae								
Average	15	7	96	690	8	5	91	467
Std.Error	2	1			1	1		
Ctenophores								
Average	22	6	88	544	4	3	88	270
Std.Error	10	1			1	1		
Oikopleura								
Average	11	3	76	249	6	4	84	366
Std.Error	4	1			2	1		

Table 4: Modified Index of Relative Importance (MIRI), average and standard error values calculated for number (N), percent number (%N), and frequency of occurrence (%FO) of individuals for the ten most important zooplankton taxa found in zooplankton tows collected inside and outside basking shark feeding areas in the Gulf of Maine. n=number of zooplankton tows collected inside and outside feeding areas.

	INSIDE TOWS (n=4)				OUTSIDE TOWS (n=4)			
Taxon	N	%N	%FO	Modified IRI	N	%N	%FO	Modified IRI
Calanus finmarchicus								
Average	506	41	100	4072	111	18	100	1753
Std.Error	382	22			101	16		
Acartia								
Average	7	6	75	445	11	5	67	349
Std.Error	4	4			6	5		
Centropages sp.								
Average	71	24	75	1823	90	20	100	2011
Std.Error	54	8			39	12		
Unknown copepod								
Average	0	1	25	13	0	0	0	0
Std.Error	0	1			0	0		
Nauplii								
Average	1	1	50	57	3	0	33	5
Std.Error	1	1			3	0		
Ostracod								
Average	21	19	75	1424	393	30	67	2016
Std.Error	9	10			374	18		
Hyperiid amphipod								
Average	27	2	50	87	17	3	67	179
Std.Error	24	1			17	3		
Megatyphines norvegica								
Average	4	1	25	14	76	12	33	393
Std.Error	4	1			76	12		
Medusae								
Average	1	1	50	52	165	10	67	643
Std.Error	1	1			163	8		
Fish eggs								
Average	4	5	50	231	11	3	67	178
Std.Error	3	3			7	2		

Table 5: Results of one-tailed paired t-tests, mean densities, and standard error (SE) of zooplankton (with average densities >5 individuals/m3) collected inside and outside basking shark feeding areas for (a) Monterey Bay and (b) British Columbia. Significant values are in bold type.

(a) Monterey Bay

Taxon	Mean density inside	SE inside	Mean density outside	SE outside	t value	P(T<=t)
Calanus pacificus	901	352	93	39	2.61	**0.02***
Acartia tonsa	17	5	23	5	-0.07	0.47
Brachyuran zoea	13	10	2	1	0.97	0.19
Crancridae zoea	9	9	1	0	0.93	0.19
Euphausia pacifica	54	23	25	13	1.47	0.1
Chaetognaths	27	10	3	1	21.64	**1.95x10-6***
Anchovy eggs	4	3	7	4	0.23	0.41

(b) British Columbia

Taxon	Mean density inside	SE inside	Mean density outside	SE outside	t value	P(T<=t)
Calanus pacificus	74	23	93	53	-0.94	0.18
Acartia sp.	19	4	17	4	0.28	0.39
Centropages abdominis	23	8	21	17	0.80	0.22
Brachyuran zoea	36	20	6	1	-0.70	0.25
Xanthidae zoea	27	17	4	1	1.61	0.06
Decapod larvae	38	20	26	14	1.37	0.09
Medusae	37	7	34	6	2.58	**0.01***
Hydromedusae	15	2	8	1	1.79	**0.04***
Ctenophores	22	10	4	1	1.92	**0.03***

Table 6: Results of one-tailed paired t-tests, mean densities, and standard error (SE) of zooplankton (with average densities >5.0 individuals/m3) collected inside and outside basking shark feeding areas for the Gulf of Maine.

Taxon	Mean density inside	SE inside	Mean density outside	SE outside	t value	P(T<=t)
Calanus finmarchicus	506	382	111	101	1.23	0.15
Acartia	7	4	11	6	-0.91	0.22
Centropages	71	54	90	39	-0.68	0.27
Hyperiid amphipod	27	24	17	17	0.67	0.27
Megatyphines norvegica	4	4	76	76	-1.30	0.14
Fish eggs	4	3	11	7	-1.15	0.17
Medusae	1	1	165	163	-1.42	0.13
Ostracod	21	9	393	393	-1.45	0.12

Table 7: Results of zooplankton comparisons, Shannon-Weiner diversity, Dominance, and Zooplankton evenness for zooplankton tows collected inside and outside feeding areas of basking sharks in (a) Monterey Bay, (b) British Columbia, and (c) Gulf of Maine.

(a) Monterey Bay

	inside feeding area	outside feeding area
Number of taxa	16	23
Shannon-Weiner diversity	0.97	1.62
Dominance	0.62	0.29
Prey eveness	0.35	0.52

(b) British Columbia

	inside feeding area	outside feeding area
Number of taxa	41	42
Shannon-Weiner diversity	2.46	2.39
Dominance	0.14	0.13
Zooplankton eveness	0.66	0.64

(c) Gulf of Maine

	inside feeding area	outside feeding area
Number of taxa	14	10
Shannon-Weiner diversity	1.59	1.83
Dominance	0.27	0.19
Zooplankton eveness	0.60	0.80

Table 8: Density (number of individuals/m3) and dominance values for *Calanus pacificus* collected near and away (a) from a basking shark feeding area off the Santa Barbara Channel Islands on 27 April 1989 and (b) in the same area during other seasons when basking sharks were absent.

(a)

	Density inside feeding area	Dominance *Calanus* /total	Density outside feeding area	Dominance *Calanus* /total
Calanus pacificus	2234.2	98%	461.5	90%
Other	46.5		50.5	

(b)

	Density		Dominance
	Calanus pacificus	Other	*Calanus* /total
Jul-89	6.5	18.2	26%
Nov-89	0.6	1.1	36%
Mar-90	7.8	10.7	42%
Apr-90	31.5	13.9	69%
Jul-90	4.4	4.9	47%
Nov-90	0.7	8.5	8%

Table 9: Results of overlap comparisons, Percent Similarity Index, Morisita-Horn Index, and Horn's Index for proportional taxa values (pi) and density (number of individuals/m3) for zooplankton tows collected inside and outside basking shark feeding areas in (a) Monterey Bay, (b) British Columbia, and (c) the Gulf of Maine.

(a) Monterey Bay

	Inside and Outside feeding area	
	proportional values (pi)	density (number/m3)
Percent Similarity Index	0.52	0.67
Morisita-Horn Index	0.70	0.89
Horn's Index	0.74	0.87

(b) British Columbia

	Inside and Outside feeding area	
	proportional values (pi)	density (number/m3)
Percent Similarity Index	0.80	0.70
Morisita-Horn Index	0.93	0.84
Horn's Index	0.95	0.90

(c) Gulf of Maine

	Inside and Outside feeding area	
	proportional values (pi)	density (number/m3)
Percent Similarity Index	0.68	0.31
Morisita-Horn Index	0.80	0.28
Horn's Index	0.87	0.54

Table 10: Modified Index of Relative Importance (MIRI), average and standard error values calculated for number (N), percent number (%N), and frequency of occurrence (%FO) of individuals for the ten most important prey taxa found in basking shark stomach contents, St. John's, Newfoundland. n= number of stomachs.

	Stomach contents (n=9)			
Taxon	N	%N	%FO	Modified IRI
Metridia longa	23	61	83	**6069**
Average	3	2		
Std.Error				
Calanus hyperboreus	13	19	31	**901**
Average	1	1		
Std.Error				
Calanus finmarchicus	6	7	22	**728**
Average	0	0		
Std.Error				
Calanus sp.	3	3	11	**309**
Average	0	0		
Std.Error				
Decapod larvae	1	3	39	**261**
Average	0	0		
Std.Error				
Metridia sp.	1	2	33	**152**
Average	0	0		
Std.Error				
Euchaeta sp.	0	1	30	**121**
Average	0	0		
Std.Error				
Amphipods	0	1	15	**105**
Average	0	1		
Std.Error				
Calanus glacialis	0	0	11	**15**
Average	0	0		
Std.Error				
Euphausiid	0	0	11	**13**
Average	0	0		
Std.Error				

Table 11: Latitude (°N) and longitude (°W) positions for zooplankton survey station sets A, B, and C surveyed in Monterey Bay from November 1991 to August 1993.

Region	Set A	Set B	Set C
North nearshore	36°53'.9 N 121°52' .0 W	36°52'.0 N 121°51'.9 W 36°56'.0 N 121°56'.9 W	36°50'.7 N 121°52'.9 W
North offshore	36°51'.3 N 121°57'.6 W		36°52'.5 N 121°59'.9 W
Central nearshore	36°48'.3 N 121°48'.5 W	36°45'.7 N 121°53'.0 W	36°47'.4 N 121°50'.5 W
Central offshore	36°46'.7 N 122°00'. 1 W	36°48'.0 N 121°56'.0 W	36°47'.5 N 121°59'.5 W
South nearshore	36°39'.2 N 121°52'.9 W	36°38'.9 N 121°53'.0 W	36°41'.9 N 121°53'.5 W
South offshore	36°41'.6 N 122°59'.0 W	36°41'.9 N 122°00'.0 W	36°43'.0 N 121°58'.0 W

Table 12: Zooplankton survey dates and station set sampled each survey for zooplankton surveys conducted in Monterey Bay from November 1991 to August 1993. An X denotes the set sampled for each corresponding survey date.

	Station Set Sampled		
Survey Date	A	B	C
11/11/91	X		
11/21/91		X	
2/4/92	X		
2/18/92		X	
4/10/92	X		
4/28/92		X	
5/28/92		X	
7/23/92	X		
10/12/92	X		
11/5/92			X
12/16/92	X		
1/11/93			X
3/3/93	X		
4/19/93			X
8/4/93	X		
8/12/93		X	
8/17/93			X

Table 13: Mean zooplankton biomass estimates (mg/m3), standard error values (SE), and sea surface temperatures (degrees C), among six regions of Monterey Bay, central nearshore, south nearshore, south offshore, central offshore, north offshore, and north nearshore from November 1991 to August 1993.

Survey Date	Region	Mean Biomass (mg/m3)	SE	degree C	Survey Date	Region	Mean Biomass (mg/m3)	SE	degree C
11/11/91	central nearshore	21.38	0.03	13.2	4/28/92	central nearshore	10.68	0.51	15.4
11/11/91	south nearshore	13.96	4.69	13.3	4/28/92	south nearshore	20.69	1.19	13.3
11/11/91	south offshore	14.59	0.00	13.3	4/28/92	south offshore	19.29	1.97	13.5
11/11/91	central offshore	18.13	0.98	13.9	4/28/92	central offshore	16.62	1.19	13.7
11/11/91	north offshore	28.03	3.82	13.7	4/28/92	north nearshore	34.18	1.80	16.8
11/11/91	north nearshore	31.30	0.04	13.9					
					5/28/92	central nearshore	16.66	1.33	15.2
11/21/91	central nearshore	23.30	1.65	12.4	5/28/92	south nearshore	65.31	5.83	15.5
11/21/91	south nearshore	27.64	7.01	12.3	5/28/92	south offshore	46.73	5.14	13.7
11/21/91	south offshore	14.51	1.65	12.1	5/28/92	central offshore	31.99	1.09	14.4
11/21/91	central offshore	14.23	0.13	12.7	5/28/92	north nearshore	68.66	33.34	14.9
11/21/91	north nearshore	128.75	85.05	12.9					
					7/23/92	central nearshore	8.53	0.65	18.4
1/31/92	central nearshore	44.58	4.02	13	7/23/92	south nearshore	32.15	7.28	16.7
					7/23/92	south offshore	11.54	1.28	12.7
2/4/92	central nearshore	21.90	2.48	13.2	7/23/92	central offshore	6.25	0.71	12.8
2/4/92	south nearshore	29.63	2.54	13.1	7/23/92	north offshore	9.56	0.87	14
2/4/92	south offshore	14.56	3.93	13.1	7/23/92	north nearshore	22.82	6.88	17.9
2/4/92	central offshore	9.80	1.08	13.2					
2/4/92	north offshore	12.73	1.07	13.7	8/12/92	central nearshore	24.50	5.65	14.1
2/4/92	north nearshore	19.41	5.36	14	8/12/92	south nearshore	24.63	9.58	13.2
					8/12/92	south offshore	35.99	5.70	12.9
2/18/92	central nearshore	10.41	1.63	13.8	8/12/92	central offshore	40.90	7.68	15.1
2/18/92	south nearshore	22.61	2.99	13.8					
2/18/92	south offshore	26.41	14.63	13.9					
2/18/92	central offshore	14.18	3.00	13.8					
4/10/92	central nearshore	8.46	1.42	15.4					
4/10/92	south nearshore	10.91	1.26	15.8					
4/10/92	south offshore	5.10	0.53	14.4					
4/10/92	central offshore	7.30	1.20	14.6					
4/10/92	north offshore	7.21	0.34	15.8					
4/10/92	north nearshore	5.02	0.77	15.7					

Table 13: (continued) Mean zooplankton biomass estimates (mg/m3), standard error values (SE), and sea surface temperatures (degrees C), among six regions of Monterey Bay, central nearshore, south nearshore, south offshore, central offshore, north offshore, and north nearshore from November 1991 to August 1993.

Survey Date	Region	Mean biomass (mg/m3)	SE	degree C	Survey Date	Region	Mean biomass (mg/m3)	SE	degree C
10/12/92	central nearshore	17.12	11.66	15.6	3/3/95	central nearshore	10.63	3.42	13.6
10/12/92	south nearshore	38.62	4.67	15.4	3/3/95	south nearshore	6.46	0.53	14.2
10/12/92	south offshore	38.43	8.36	15.2	3/3/95	south offshore	4.98	0.79	13.6
10/12/92	central offshore	39.75	12.27	15.4	3/3/95	central offshore	4.11	1.94	13.4
10/12/92	north offshore	45.25	1.09	15.3	3/3/95	north nearshore	8.38	0.91	13.8
10/12/92	north nearshore	43.98	6.40	15.2	3/3/95	north offshore	4.90	0.69	13.7
10/29/92	central nearshore	8.90	1.43	15.9	4/19/93	central nearshore	10.17	0.68	12.7
					4/19/93	south nearshore	23.41	1.59	12.7
11/5/92	central nearshore	3.16	0.64	15.9	4/19/93	south offshore	27.64	2.89	12.1
11/5/92	south nearshore	6.24	1.08	16.1	4/19/93	central offshore	50.38	3.62	12.6
11/5/92	south offshore	6.72	0.72	16.1	4/19/93	north nearshore	28.38	2.72	13.1
11/5/92	central offshore	10.25	1.89	15.9					
11/5/92	north nearshore	9.04	1.96	16.2	8/4/93	central nearshore	65.84	15.06	16.5
					8/4/93	south nearshore	31.26	3.96	17.1
12/16/92	central nearshore	5.14	0.87	14.1	8/4/93	south offshore	52.67	5.37	17.1
12/16/92	south nearshore	8.25	0.64	14.1	8/4/93	central offshore	47.10	2.41	16.7
12/16/92	south offshore	8.26	3.90	14.3	8/4/93	north offshore	58.42	4.67	17.2
12/16/92	central offshore	4.58	1.18	14.2	8/4/93	north nearshore	132.98	2.72	17.7
12/16/92	north offshore	4.95	0.45	14.2					
12/16/92	north nearshore	5.50	0.32	14.1	8/17/93	central nearshore	4.81	0.85	16.2
					8/17/93	south nearshore	11.88	6.95	17
1/11/93	central nearshore	19.18	5.15	12.7	8/17/93	south offshore	3.63	1.68	17.4
1/11/93	south nearshore	7.30	0.92	12.8	8/17/93	central offshore	2.99	1.23	16.7
1/11/93	south offshore	13.77	3.31	13.1	8/17/93	north nearshore	7.60	3.69	18.3
1/11/93	central offshore	10.47	1.57	13					
1/11/93	north nearshore	8.27	2.28	12.6					

Table 14: ANOVA table for temporal and spatial differences of zooplankton biomass in Monterey Bay from November 1991-August 1993.

Source	Sum of Squares	DF	Mean Square	F-Ratio	P
Year	396	1	396	0.64	0.424
Season	4481	2	2241	3.64	***0.029**
Region	2523	2	1262	2.05	0.132
Site	864	1	864	1.40	0.238
Year*Season	3211	2	1606	2.61	0.077
Year*Region	354	2	177	0.29	0.751
Year*Site	2875	1	2875	4.67	***0.032**
Season*Region	4375	4	1094	1.78	0.136
Season*Site	127	2	63	0.10	0.902
Region*Site	807	2	403	0.66	0.521
Year*Season*Region	2758	4	690	1.12	0.349
Year*Season*Site	1487	2	744	1.21	0.302
Year*Region*Site	1520	2	760	1.23	0.294
Season*Region*Site	939	4	235	0.38	0.822
Year*Season*Region*Site	2178	4	544	0.88	0.475
Error	95470	155	616		

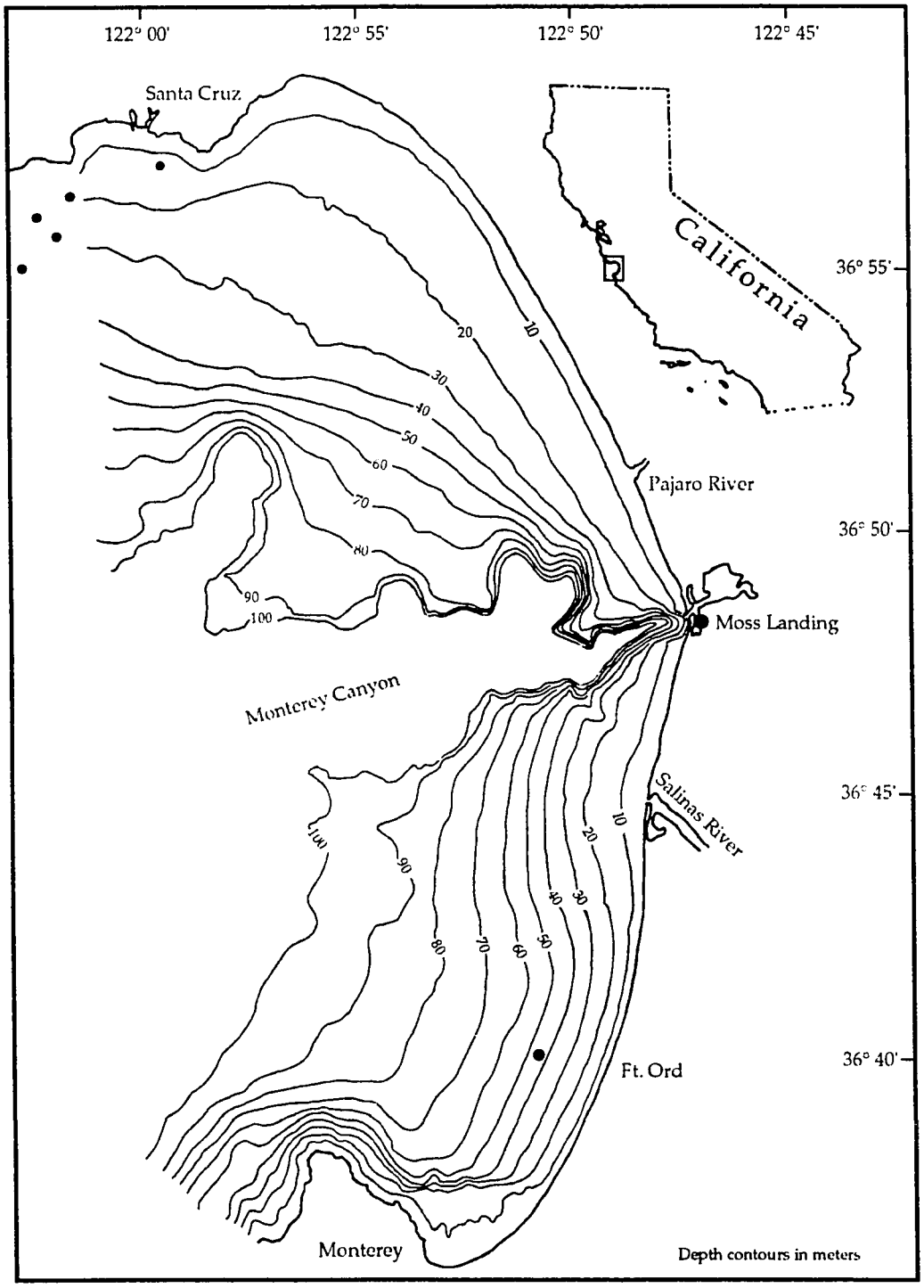

Fig. 1: Basking shark feeding areas (•) in northern Monterey Bay, California where zooplankton tows were collected in December 1991 and off Fort Ord in February 1991.

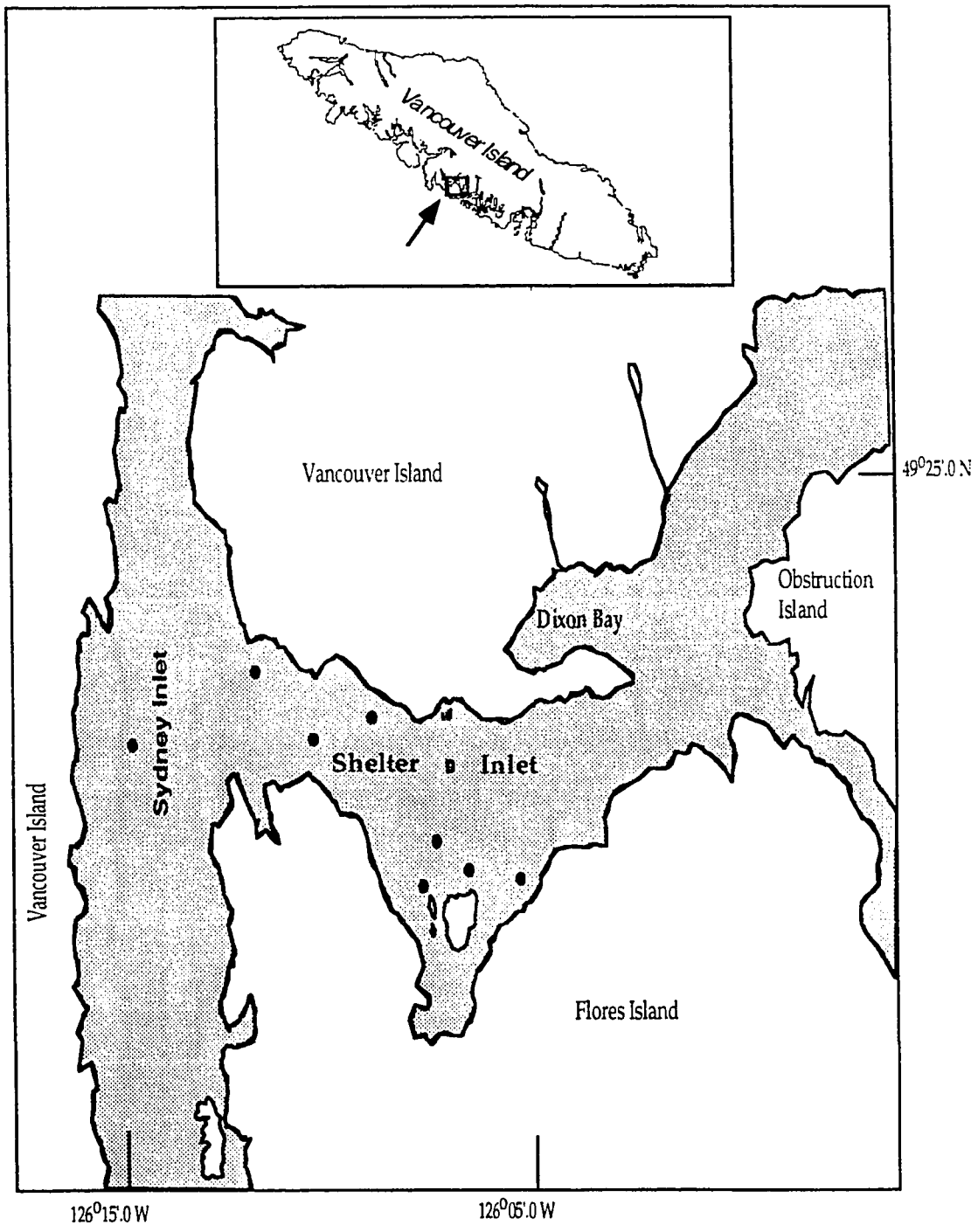

Fig. 2: Basking shark feeding areas (•) in Clayoquot Sound, Vancouver Island, British Columbia where zooplankton tows were collected from June-September 1993.

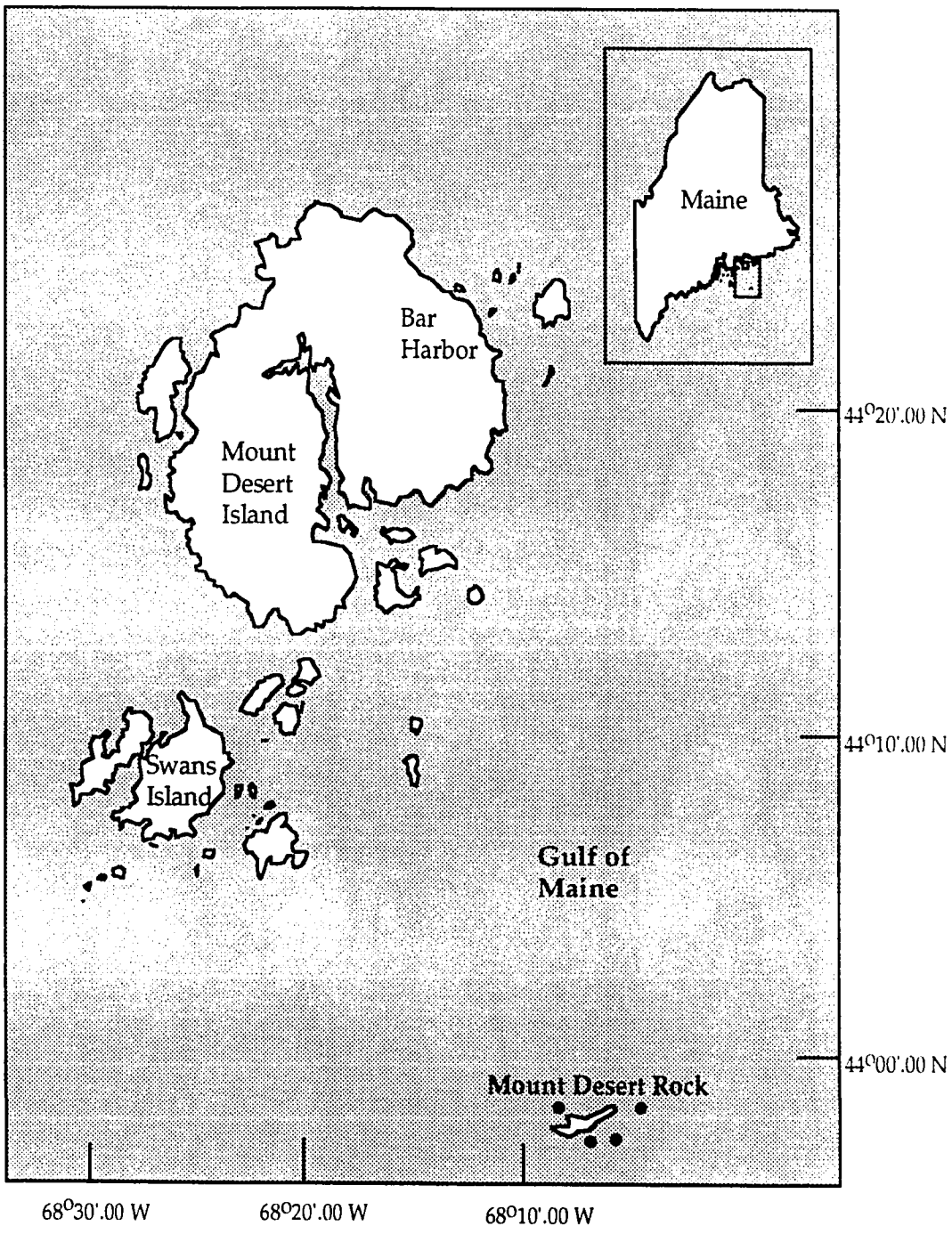

Fig. 3: Basking shark feeding areas (•) off Mount Desert Rock in the Gulf of Maine where zooplankton tows were collected from August to September 1993.

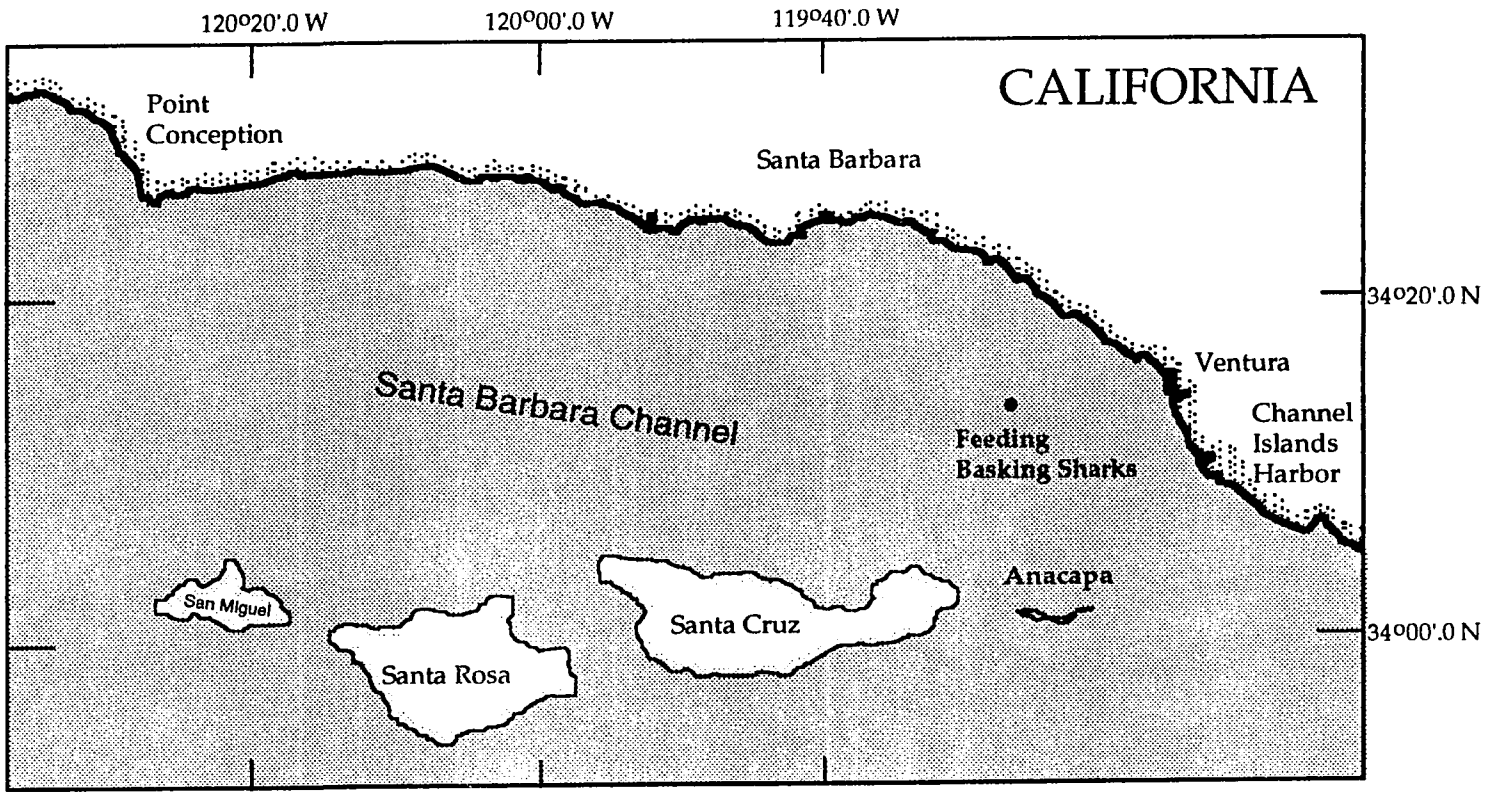

Fig. 4. A basking shark feeding area (•) off the Santa Barbara Channel Islands, California. Zooplankton tows were opportunistically collected during CalCOFI cruise 8904 on 27 April 1989.

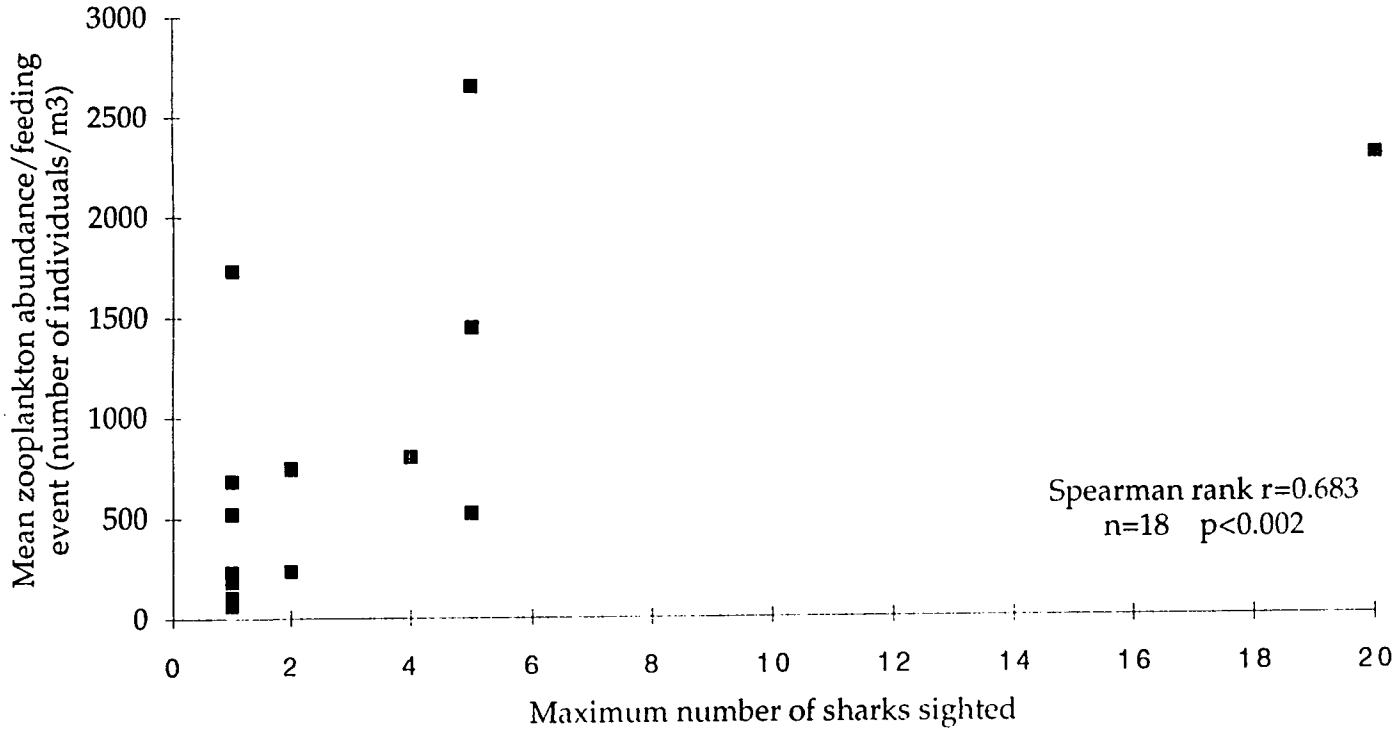

Fig. 5. Relationship between number of sharks sighted feeding at the surface and mean zooplankton abundance/feeding event (number of individuals/m3 water volume filtered).

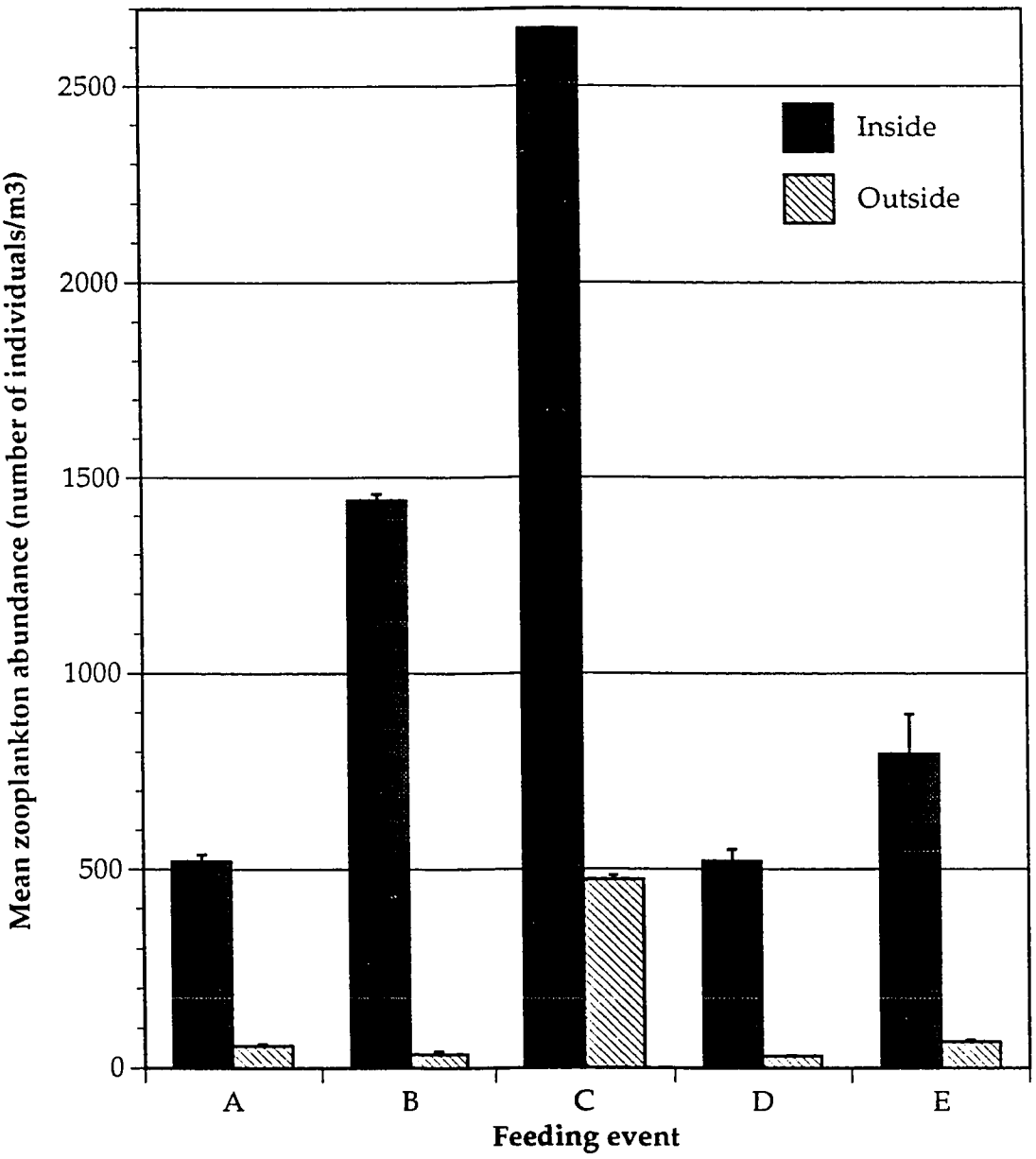

Fig. 6: Zooplankton abundance (number of individuals/m3 water volume filtered) inside and outside feeding areas of basking sharks during five feeding events in Monterey Bay, California, December, 1991. Vertical lines represent standard error.

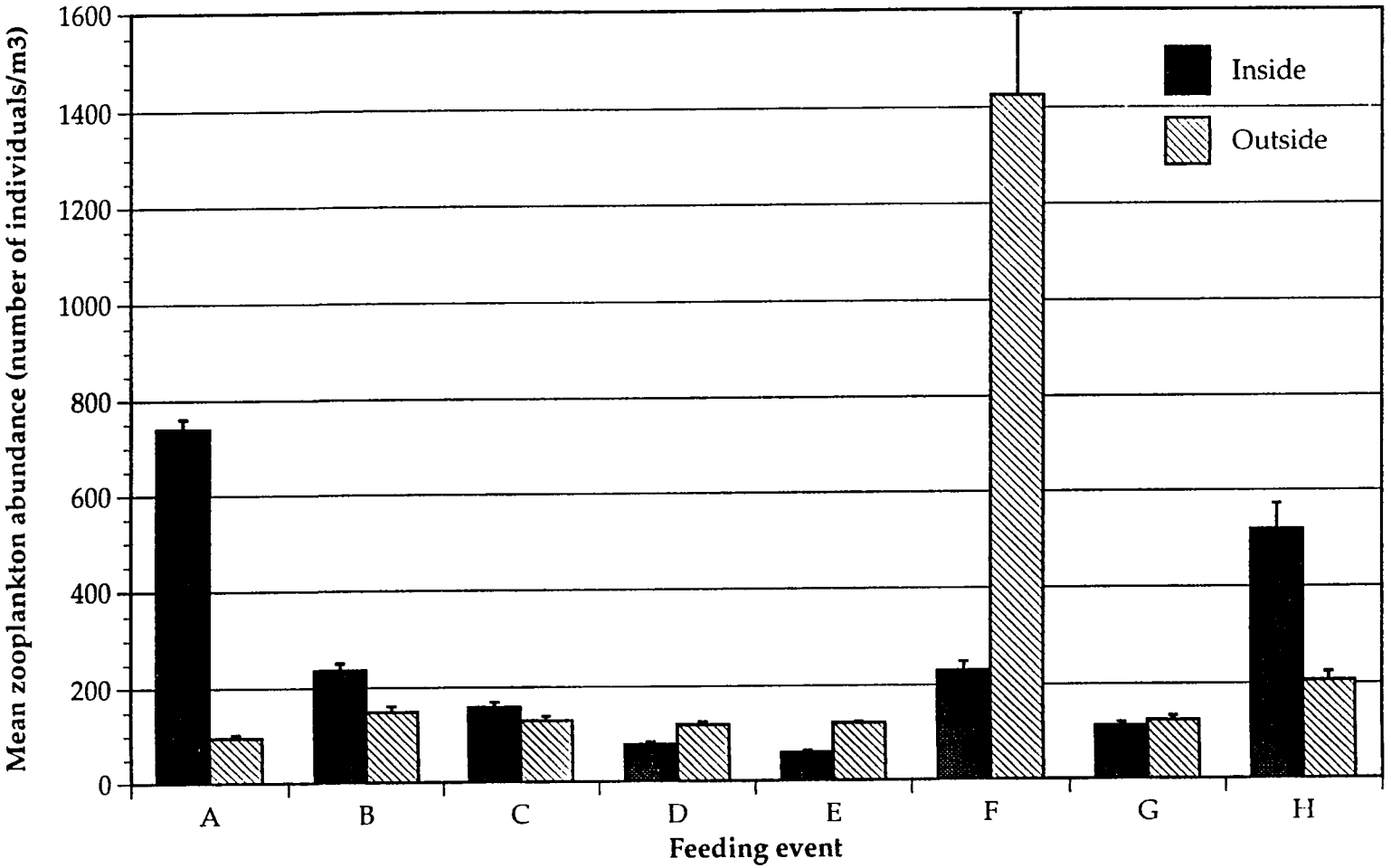

Fig. 7: Zooplankton abundance (number of individuals/m3 water volume filtered) inside and outside feeding areas of basking sharks during eight feeding events in Clayoquot Sound, British Columbia, June-September 1993. Vertical lines represent standard error.

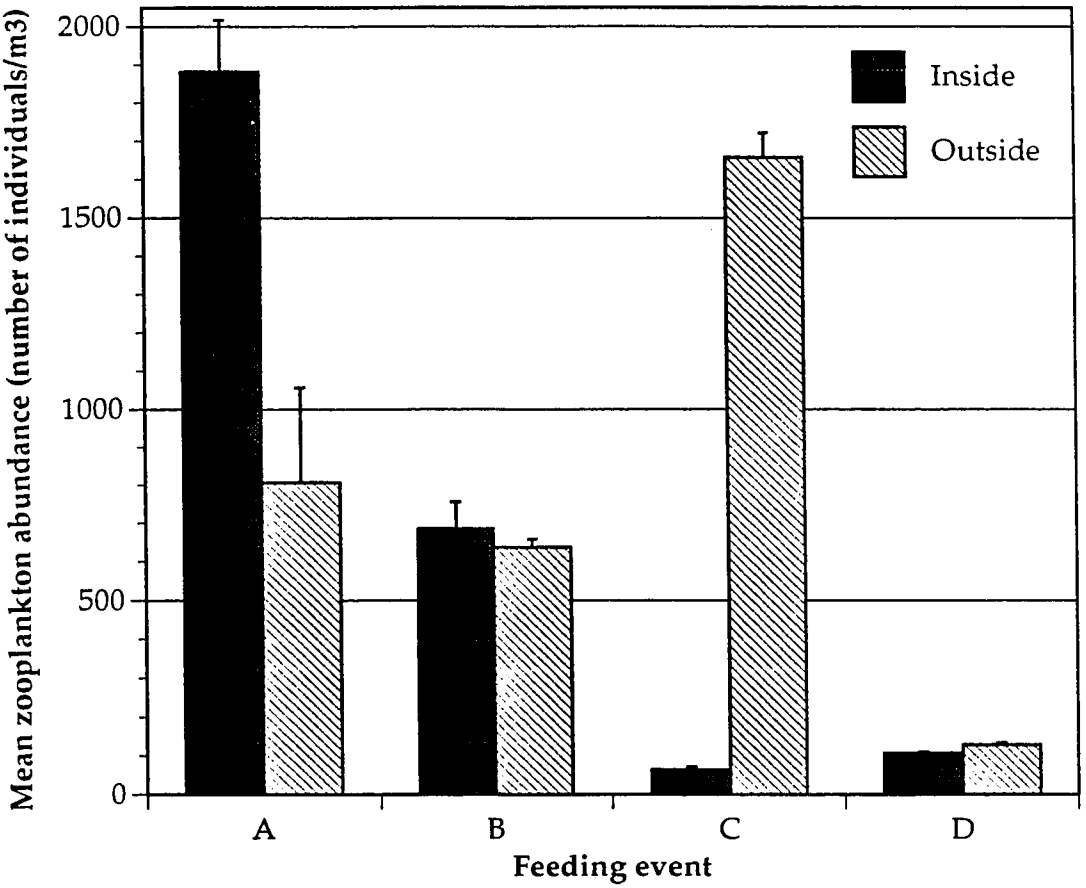

Fig. 8: Zooplankton abundance (number of individuals/m3 water volume filtered) inside and outside basking shark feeding areas during four feeding events in the Gulf of Maine, August-September, 1993. Vertical lines represent standard error.

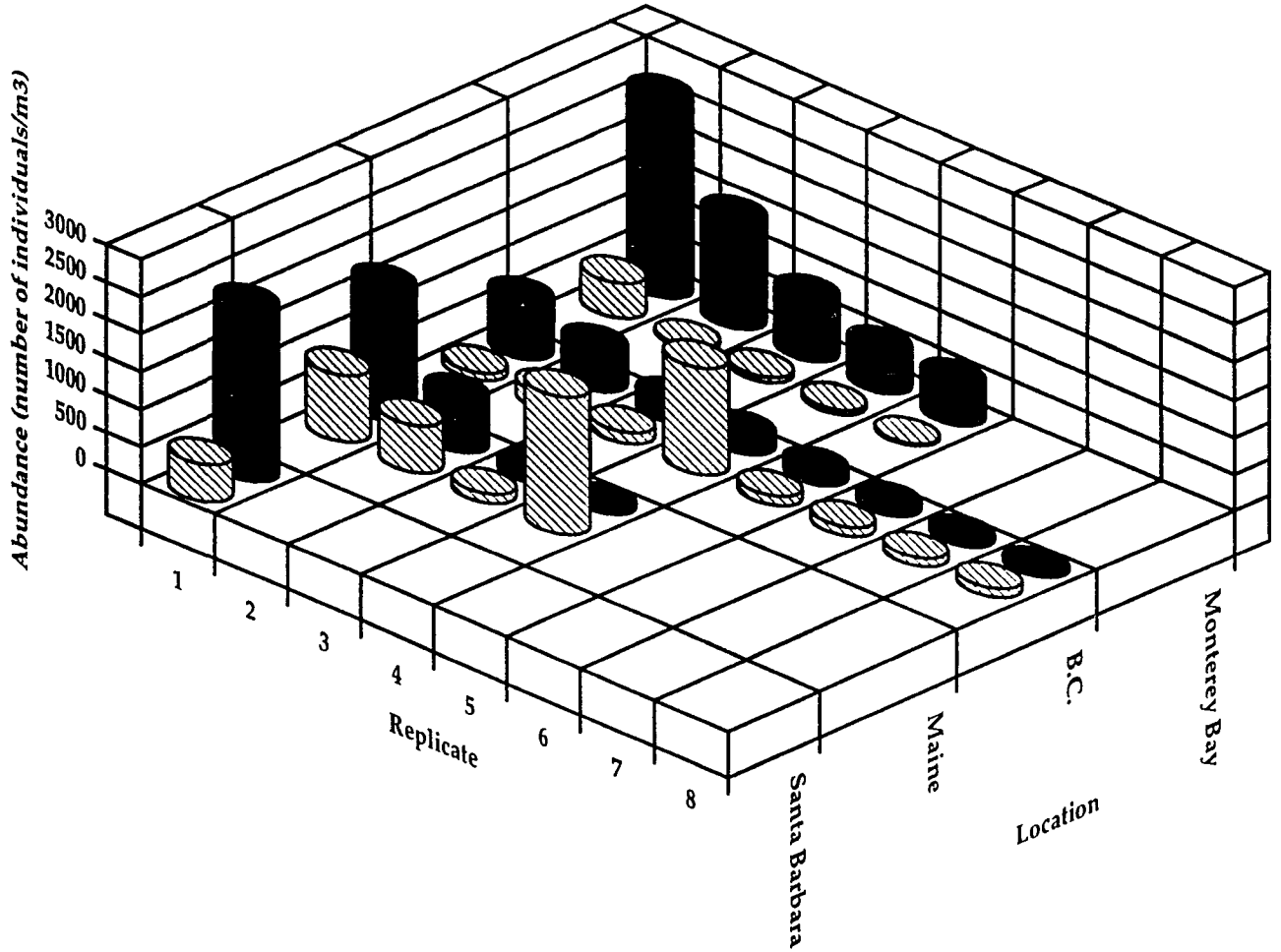

Fig. 9: Comparison of zooplankton abundance inside (stippled) and outside (hatched) basking shark feeding areas among four locations: Monterey Bay, British Columbia (B.C.), Gulf of Maine, and the Santa Barbara Channel Islands.

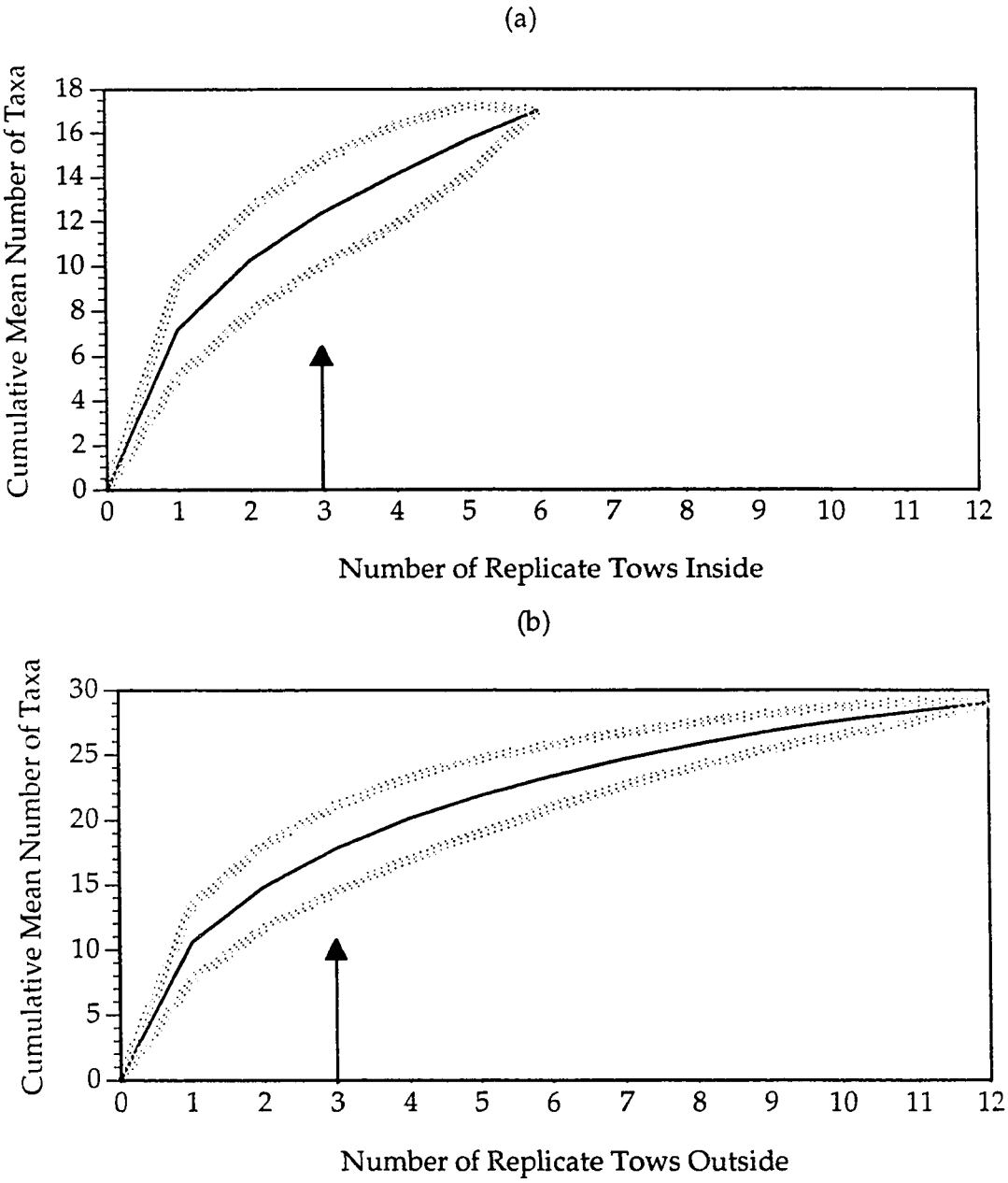

Fig. 10. Cumulative mean number of taxa +/- standard deviation (hatched lines) for zooplankton tows collected inside (a) and outside (b) basking shark feeding areas in Monterey Bay, California. Mean and SD values were calculated from 1000 random arrangements of sample data. Arrow indicates actual number of replicates collected.

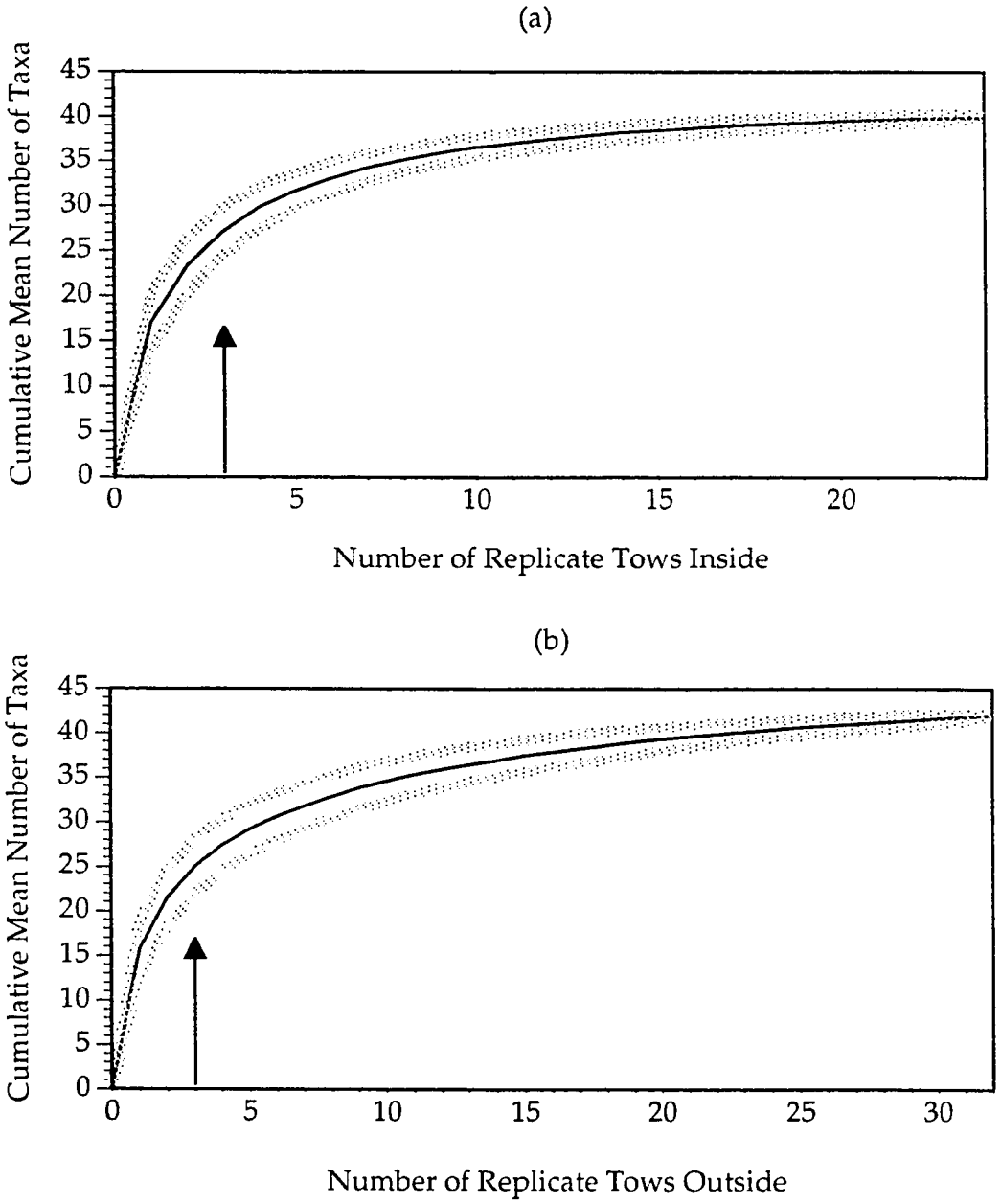

Fig. 11. Cumulative mean number of taxa +/- standard deviation (hatched lines) for zooplankton tows collected inside (a) and outside (b) basking shark feeding areas in Clayoquot Sound, British Columbia. Mean and SD values were calculated from 1000 random arrangements of sample data. Arrow indicates actual number of replicates collected.

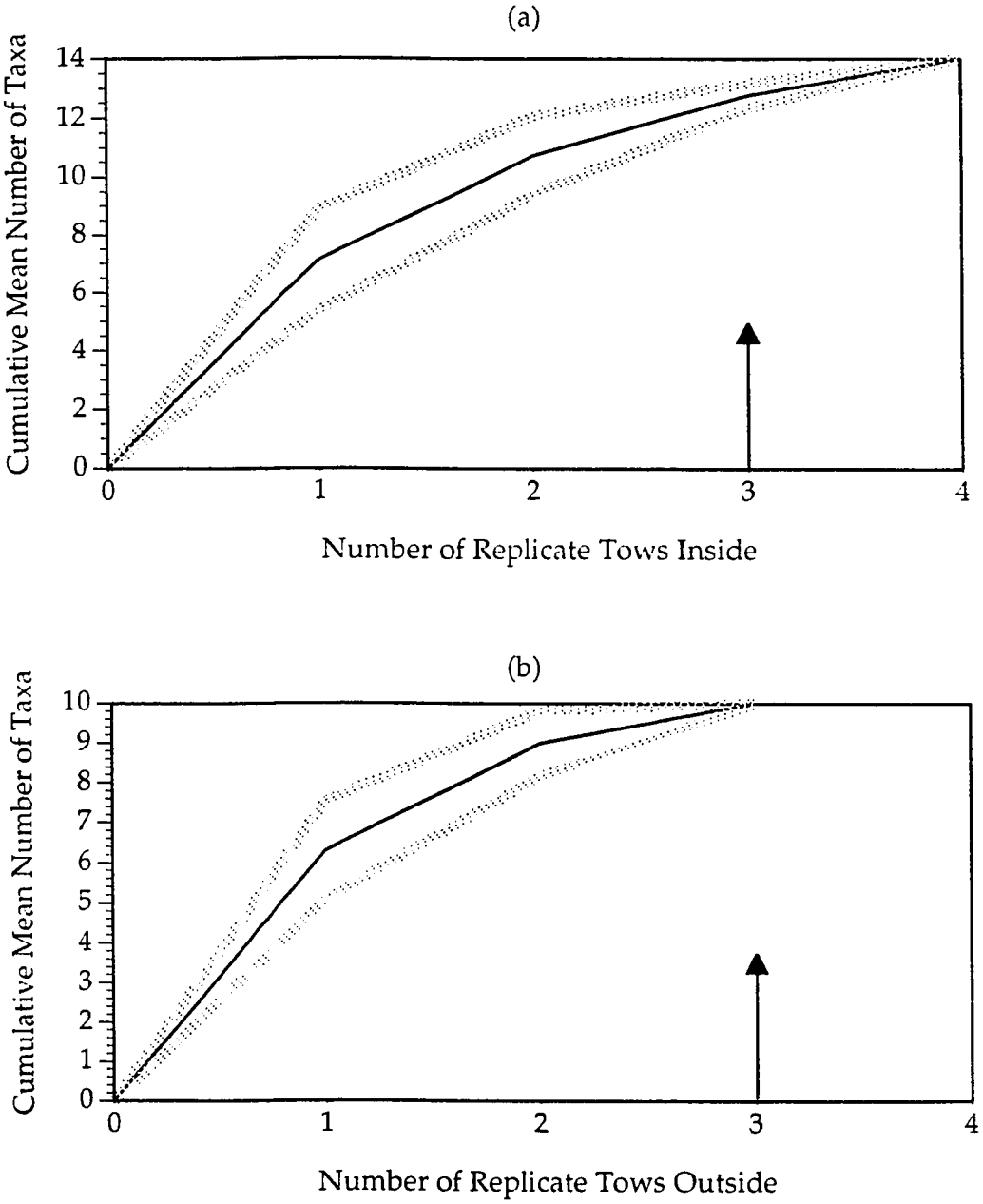

Fig. 12. Cumulative mean number of taxa +/- standard deviation (hatched lines) for zooplankton tows collected inside (a) and outside (b) basking shark feeding areas in the Gulf of Maine. Mean and SD values were calculated from 1000 random arrangements of sample data. Arrow indicates actual number of replicates collected.

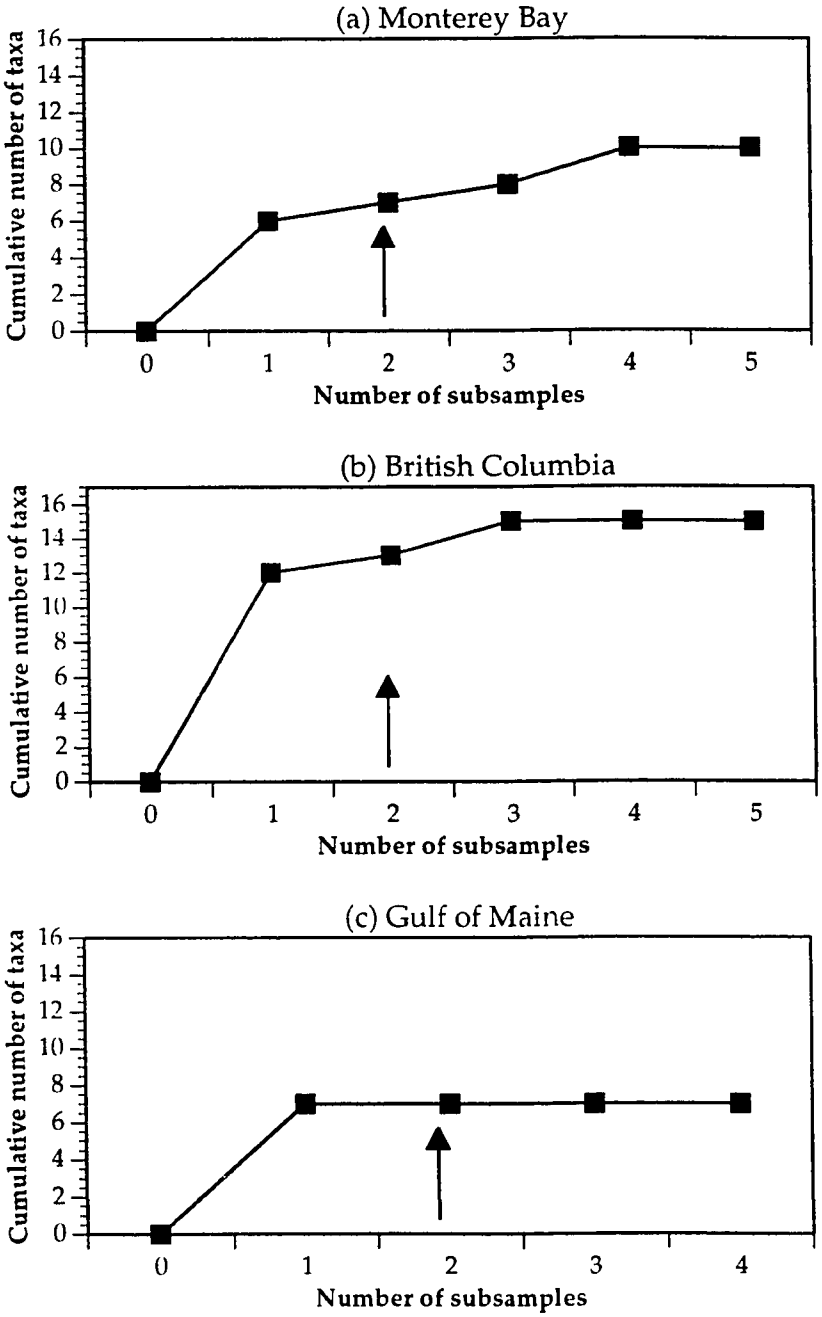

Fig. 13. Cumulative number of taxa for subsamples from one replicate zooplankton tow collected in basking shark feeding areas from (a) Monterey Bay, (b) British Columbia, and the (c) Gulf of Maine. Arrow indicates actual number of subsamples collected.

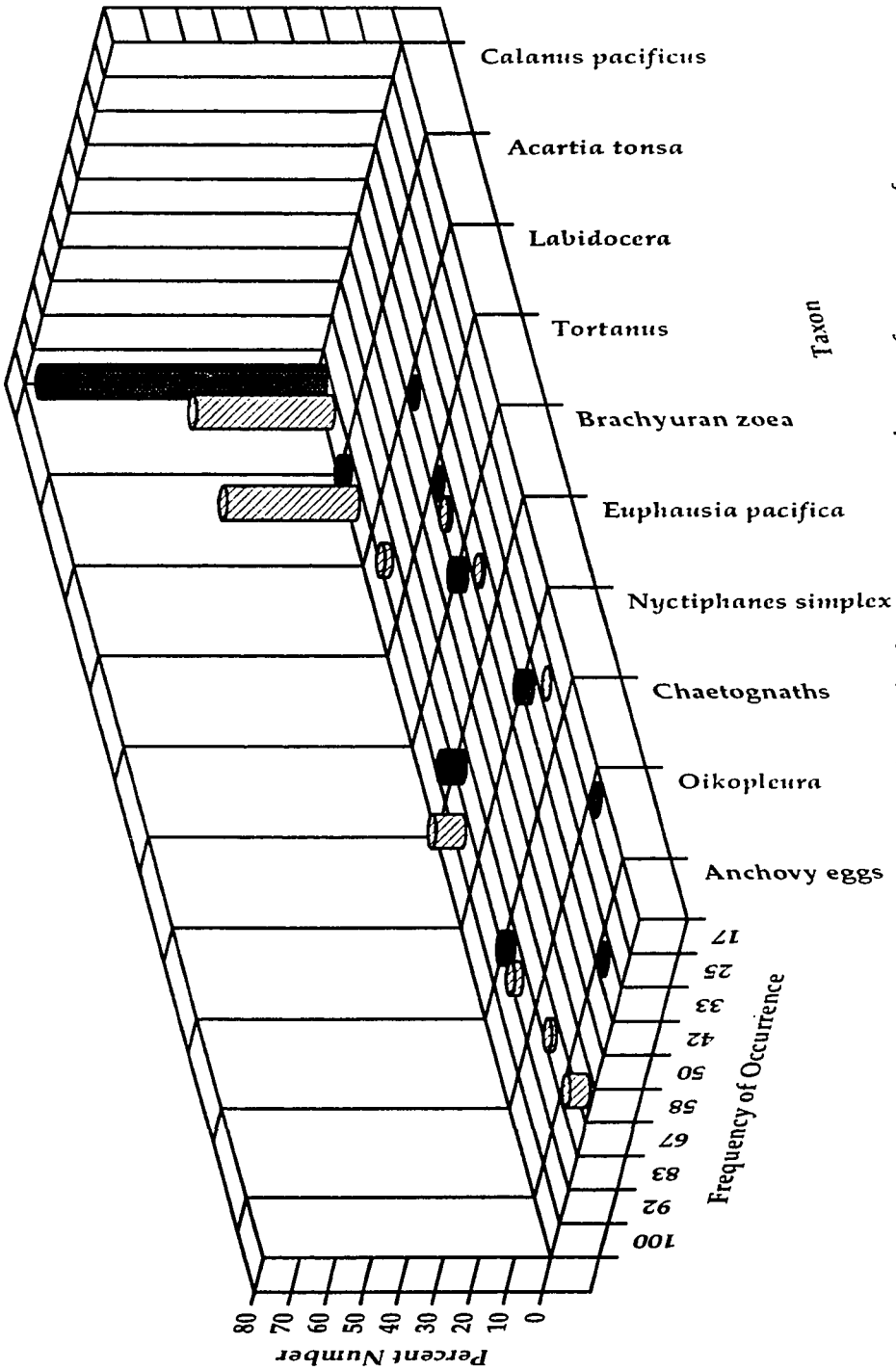

Fig. 14: Modified Index of Relative Importance (MIRI) graphed as percent number vs. frequency of occurrence for the ten most important prey taxa found inside (stippled) and outside (hatched) basking shark feeding areas in Monterey Bay, California.

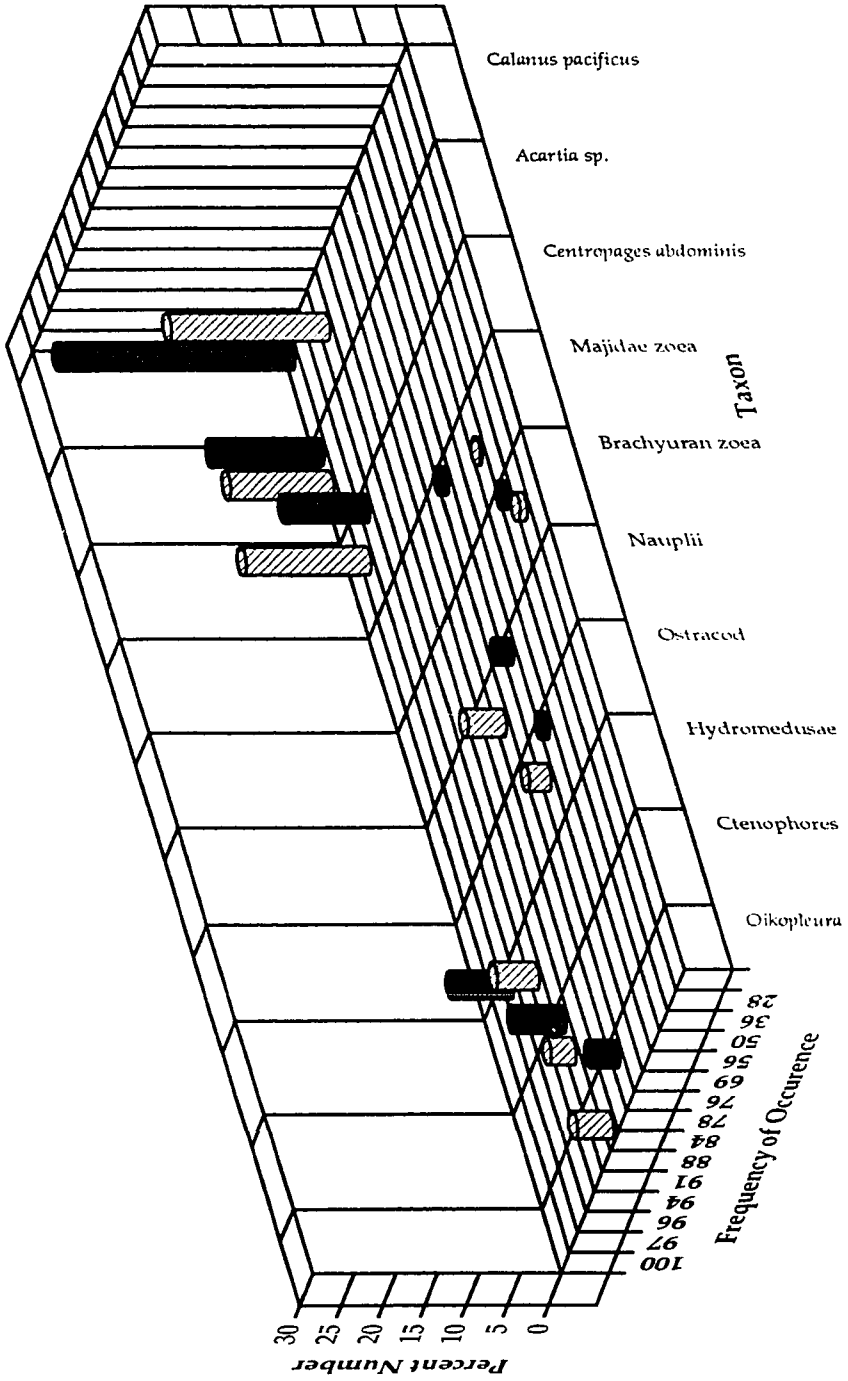

Fig. 15: Modified Index of Relative Importance (MIRI) graphed as percent number vs. frequency of occurrence for the ten most important prey taxa found inside (stippled) and outside (hatched) basking shark feeding areas in Clayoquot Sound, British Columbia.

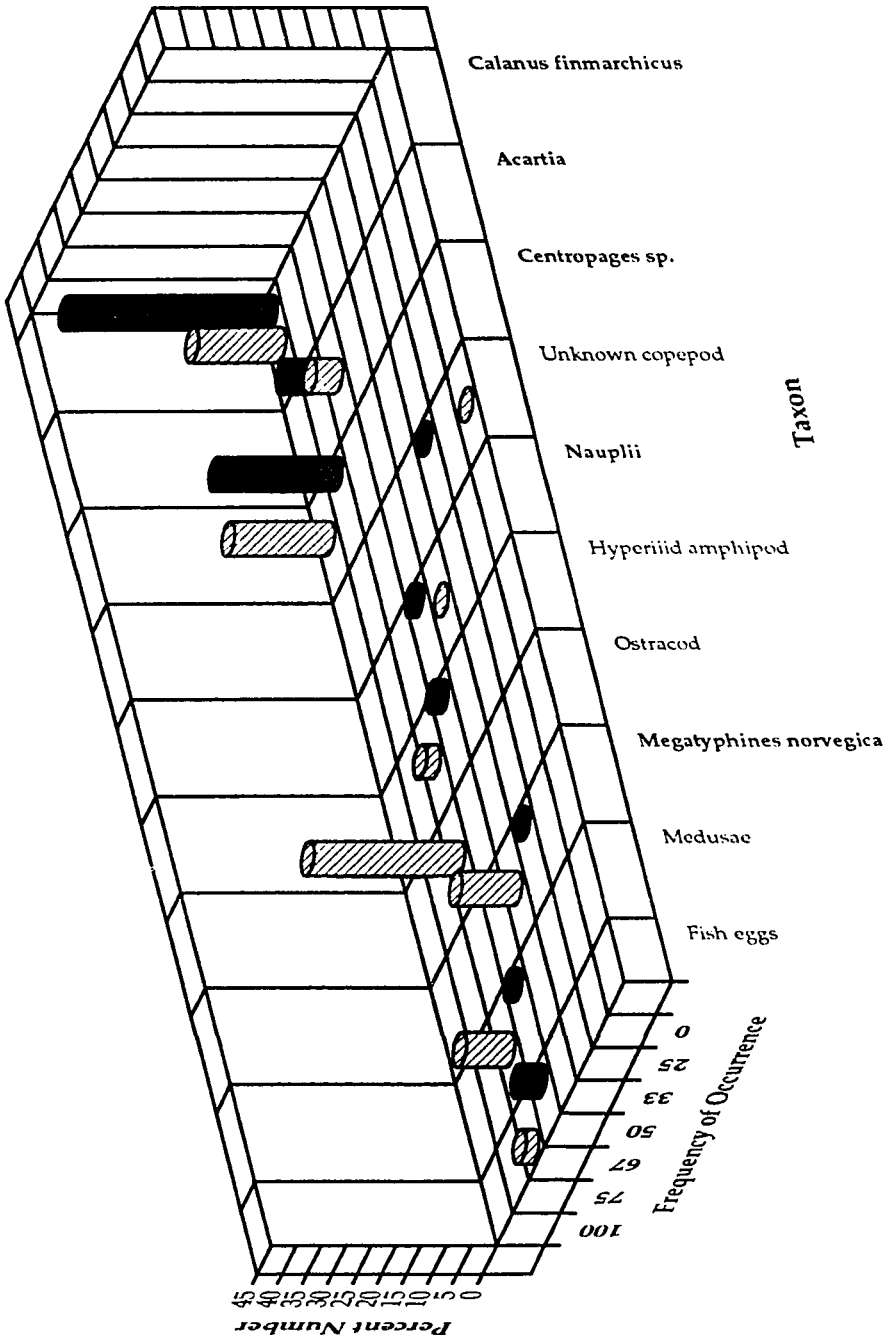

Fig. 16: Modified Index of Relative Importance (MIRI) graphed as percent number vs. frequency of occurrence for the ten most important prey taxa found inside (stippled) and outside (hatched) basking shark feeding areas in the Gulf of Maine.

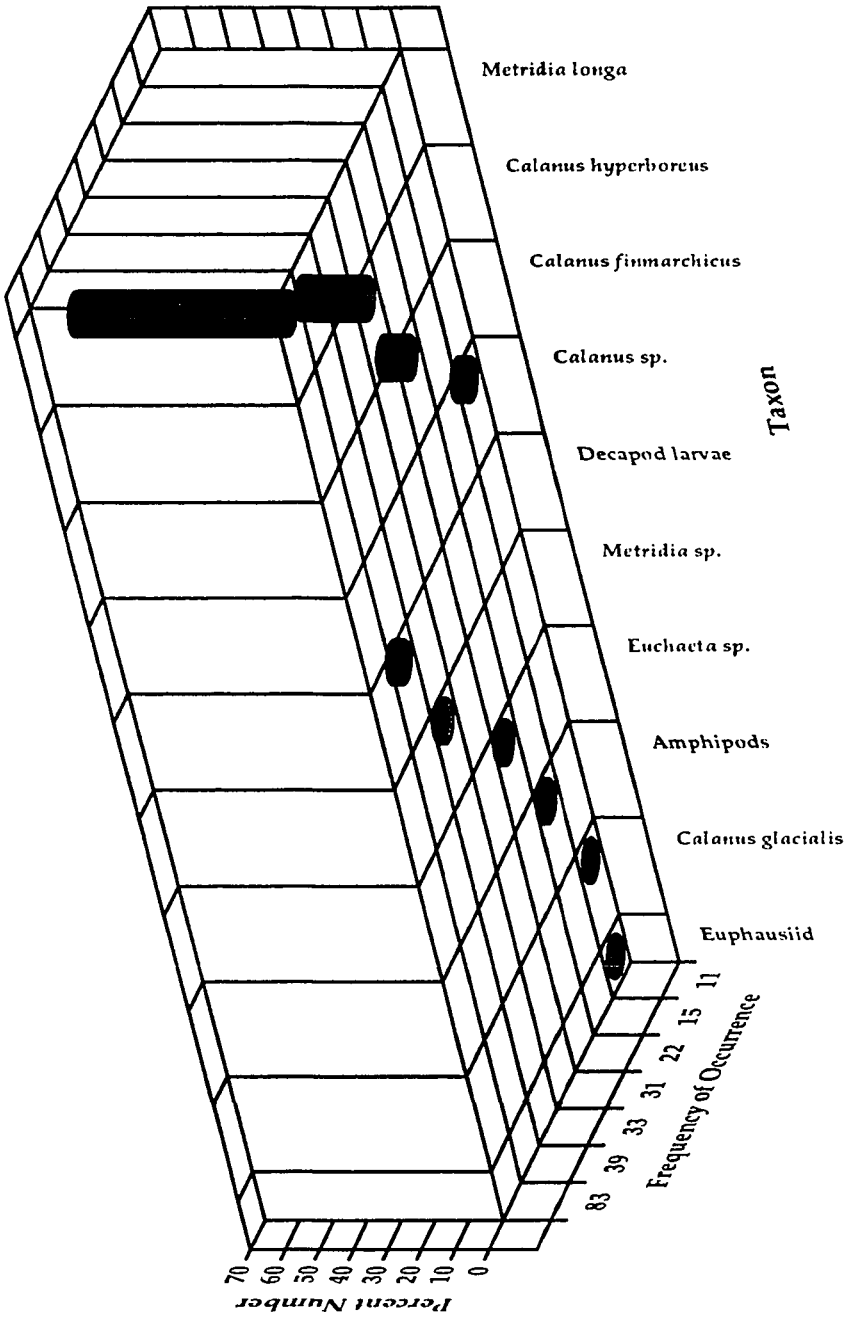

Fig. 17: Modified Index of Relative Importance (MIRI) graphed as percent number vs. frequency of occurrence for the ten most important prey taxa identified from basking shark stomach contents (n=9) collected off St. John's, Newfoundland.

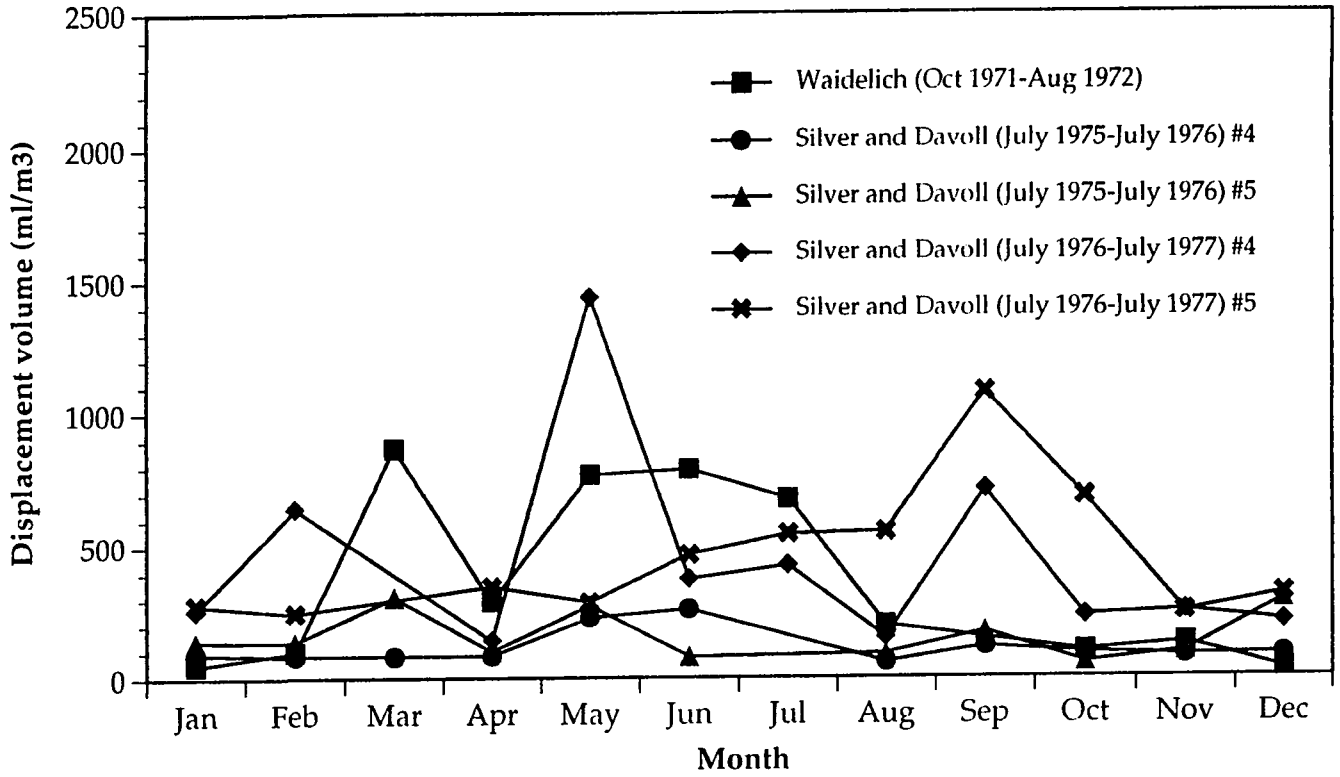

Fig. 18. Historical zooplankton data collected in Monterey Bay from Oct 1971-Aug 1972 (Waidelich, 1976) and from July 1975-July 1977 (two stations, #4 and #5; Silver and Davoll, 1976,1977). Biomass measured as displacement volume (ml/m3).

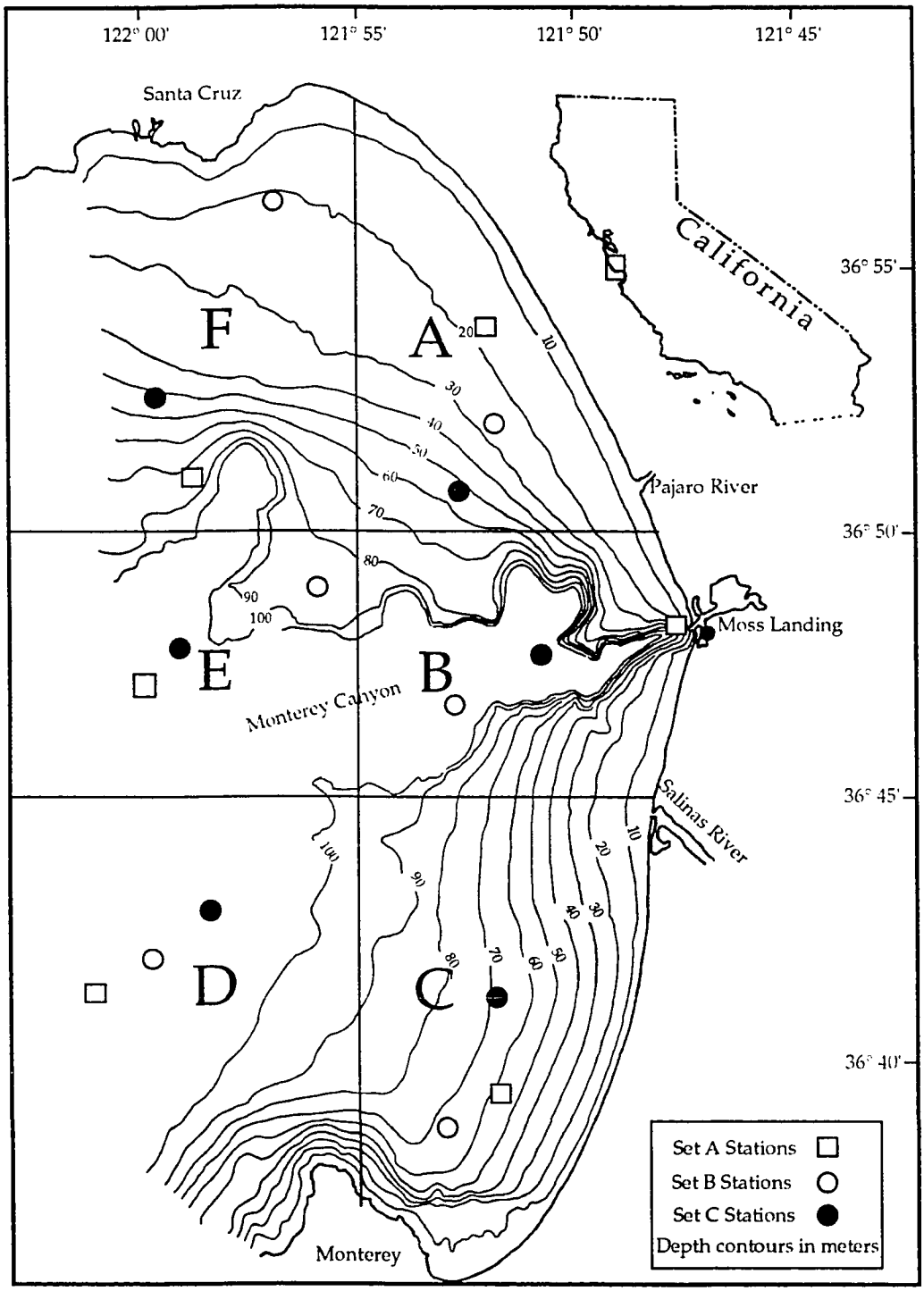

Fig. 19: Six regional divisions of the Monterey Bay study area, a) nearshore north bay, b) nearshore central bay, c) nearshore south bay, d) offshore south bay, e) offshore central bay, and f) offshore north bay.

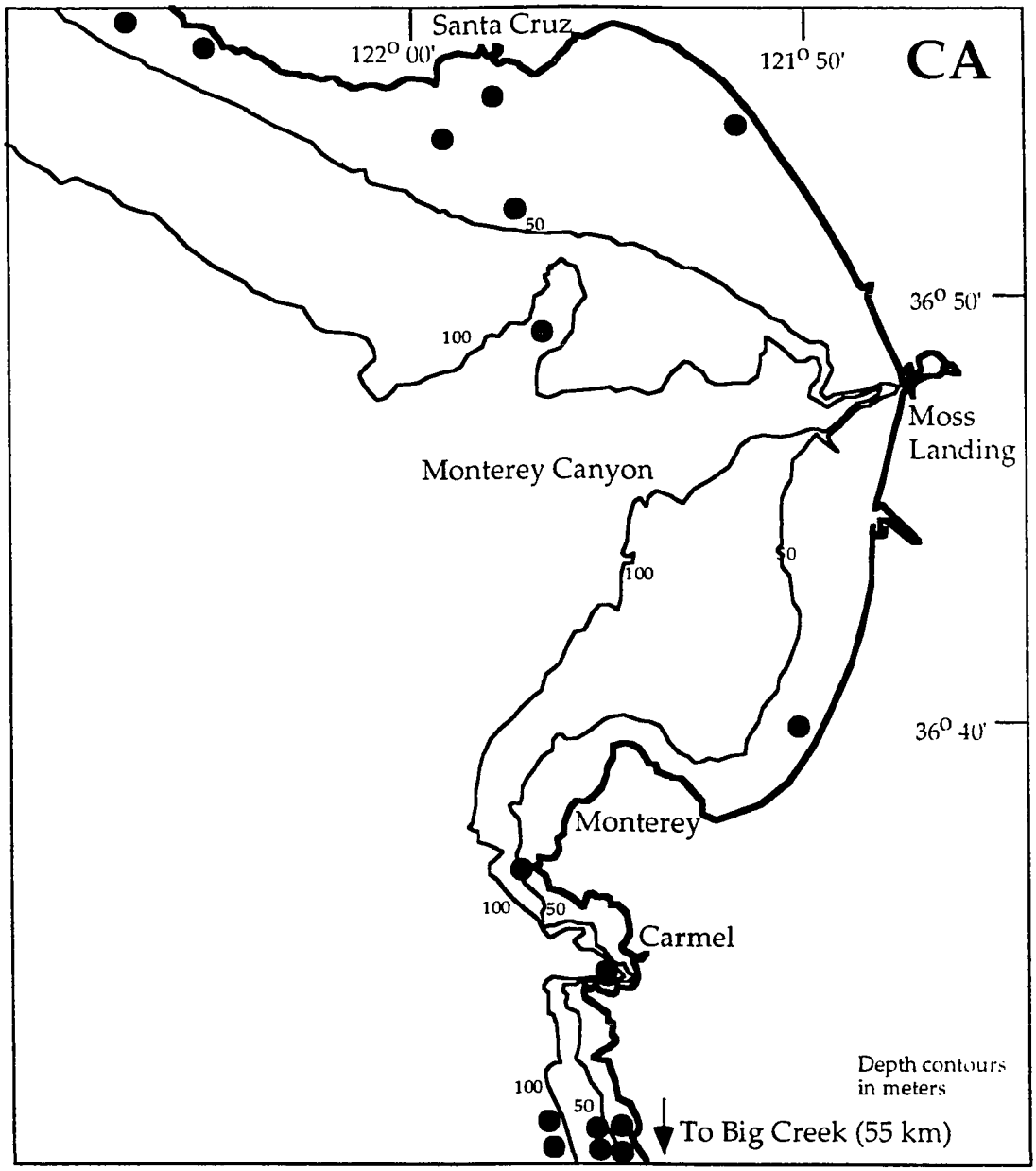

Fig. 20: Opportunistic sightings (●) of basking sharks (n=16), reported in the Monterey Bay area during the study period, November 1991- August 1993. Sightings located in the southernmost portion of the map occurred off Big Creek, Big Sur, and Piedras Blancas, CA.

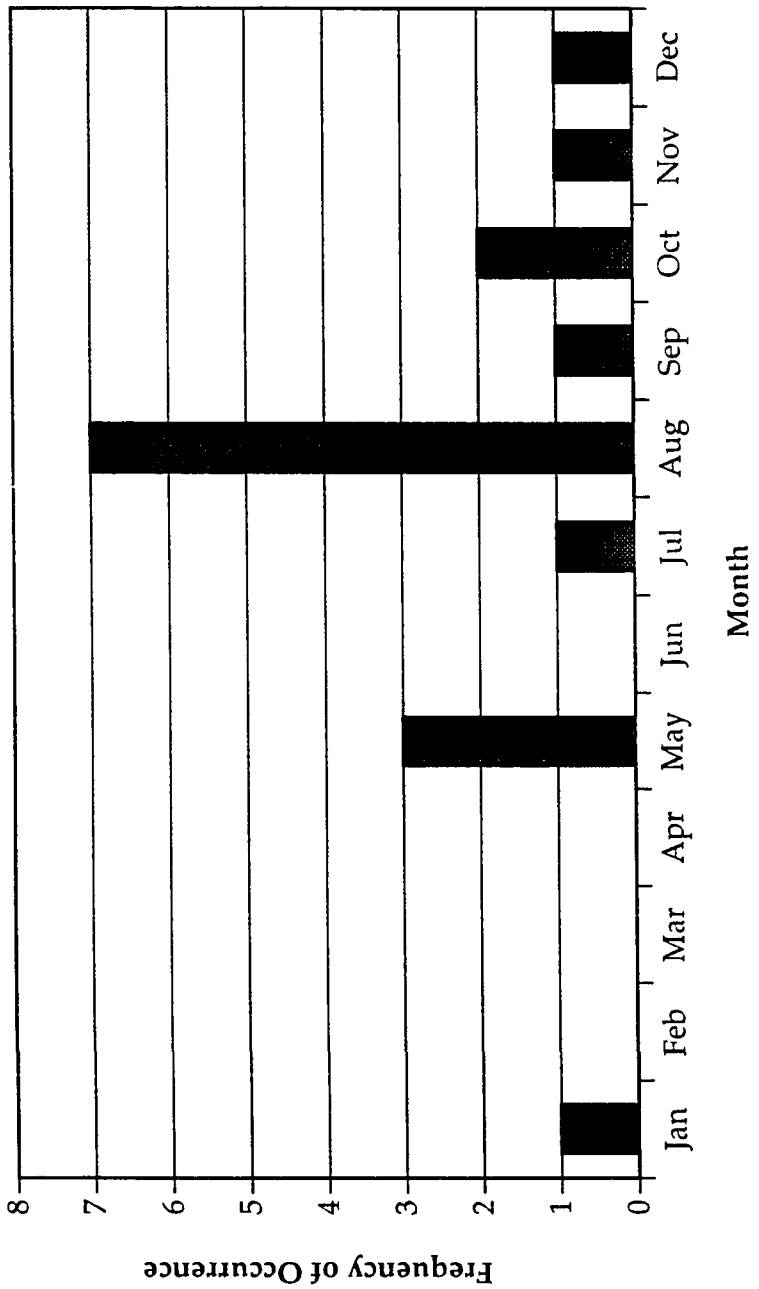

Fig. 21. Monthly occurrence of opportunistic basking shark sightings recorded from November 1991 to August 1993 in the Monterey Bay area.

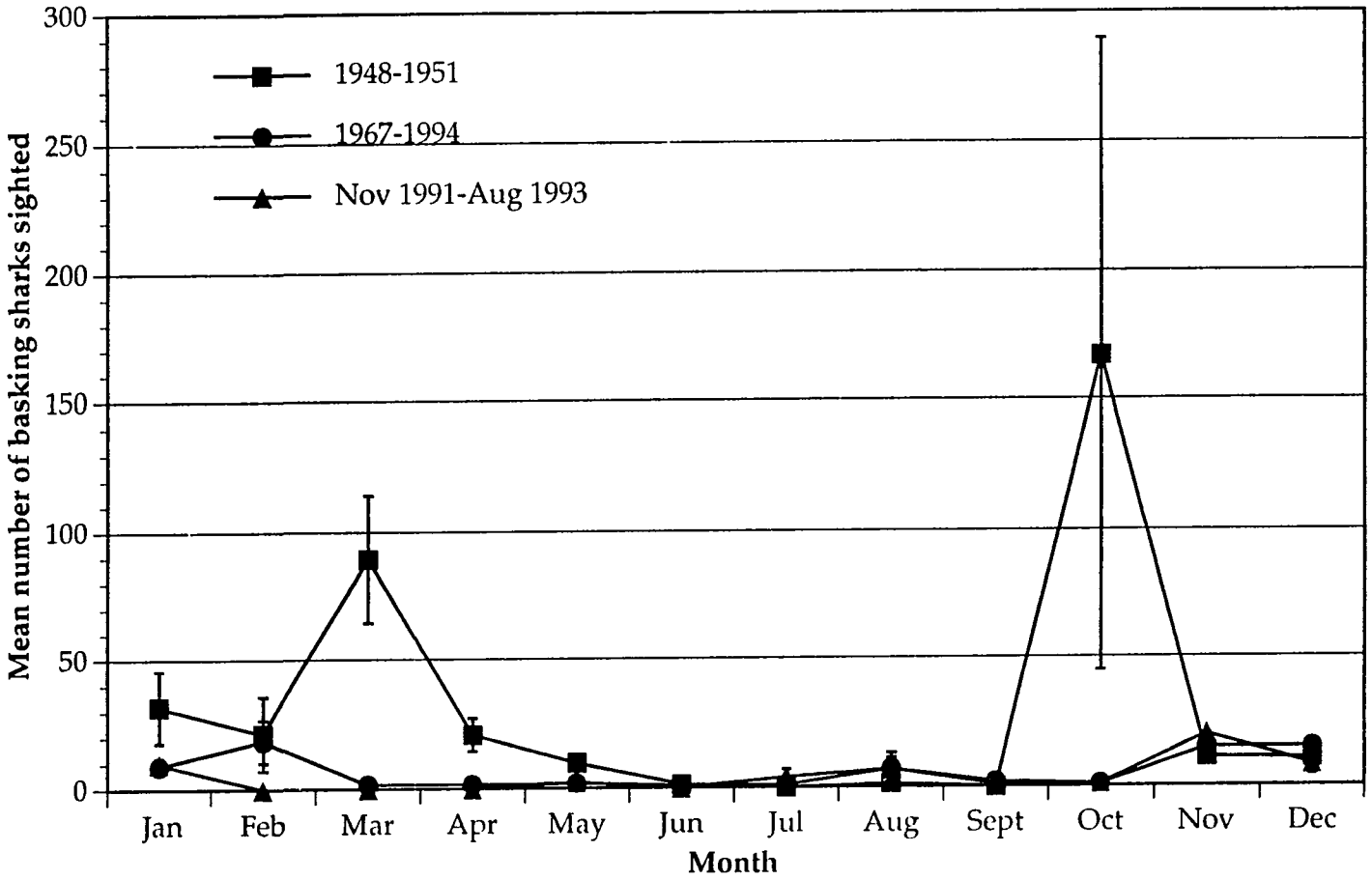

Fig. 22. Monthly sightings of basking sharks (+/- standard error) in Monterey Bay, California for (a) 1948-1951, recorded by aerial fish spotter, Edward Durden; (b) 1967-1994, opportunistically recorded by Alan Baldridge and Robert Lea; and (c) Nov 1991-Aug 1993, opportunistically recorded for this study.

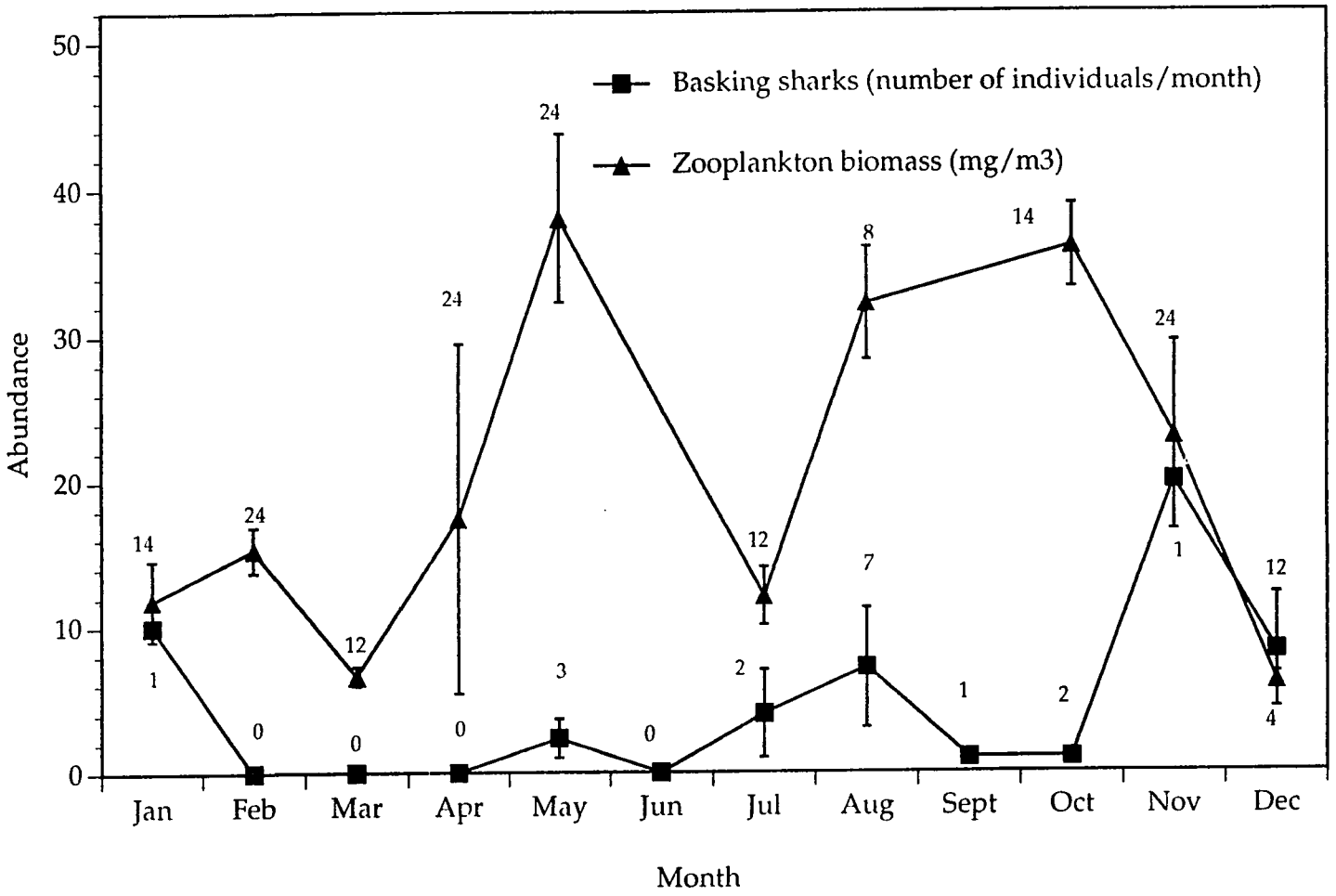

Fig. 23. Monthly sightings of basking sharks (number of individuals +/- standard error) and monthly zooplankton biomass (mg/m3) estimates from November 1991-August 1993 in Monterey Bay, California. Sample sizes are reported for each data point.

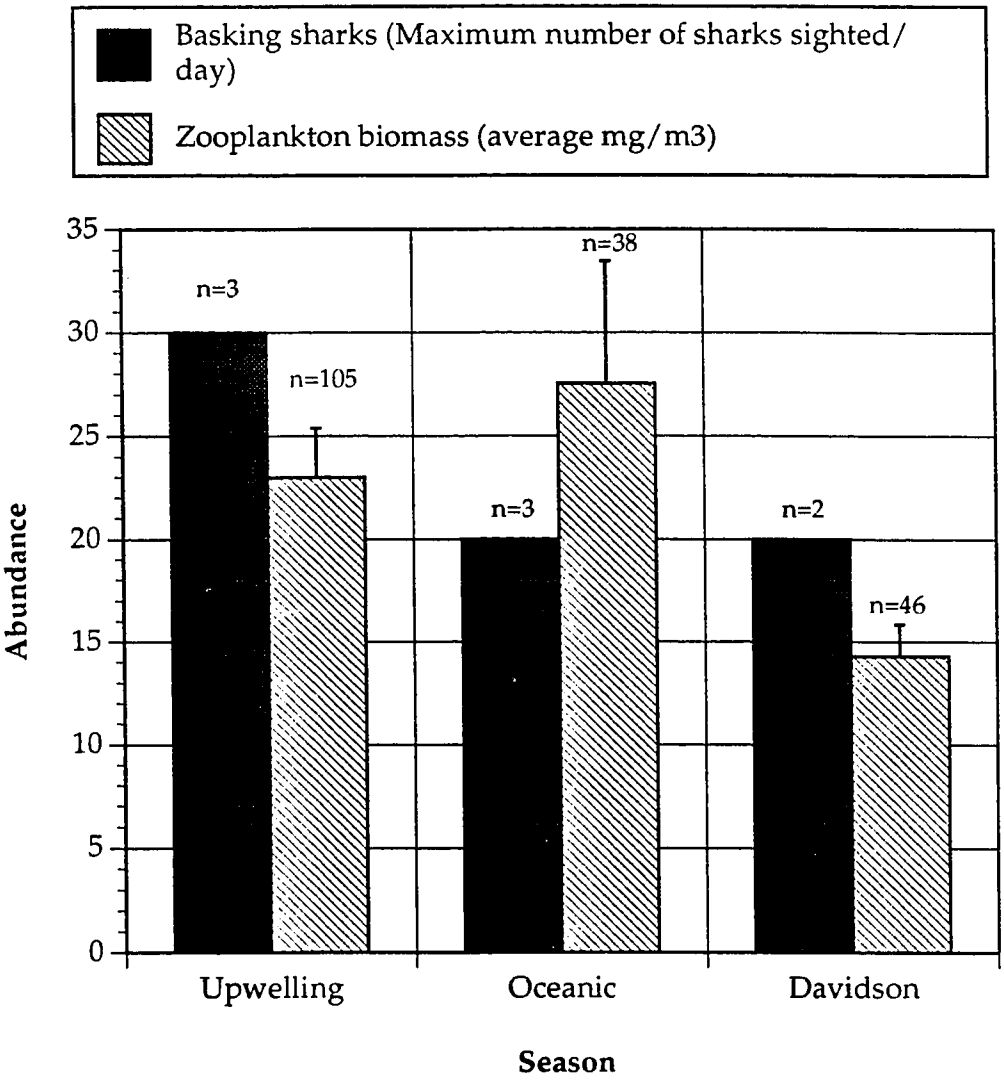

Fig. 24. Maximum number of basking sharks sighted per day and average zooplankton biomass (mg/m3) among three seasons in Monterey Bay, California, from November 1991-August 1993. Standard error reported.

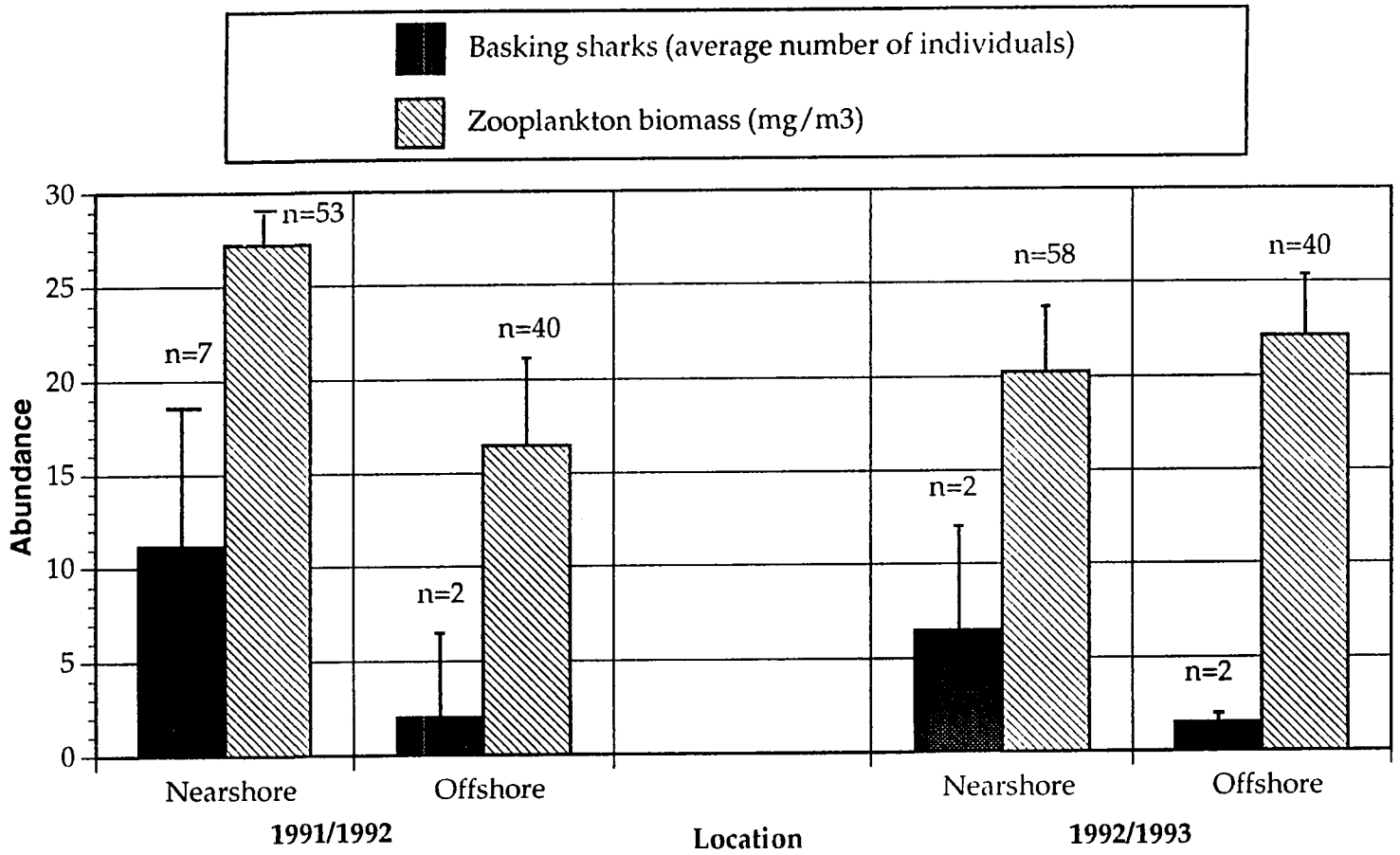

Fig. 25. Mean abundance of basking sharks (number of individuals) and zooplankton (mg/m3) (+/- standard error) between nearshore and offshore areas of Monterey Bay, California for each sampling year, 1991/1992 and 1992/1993.

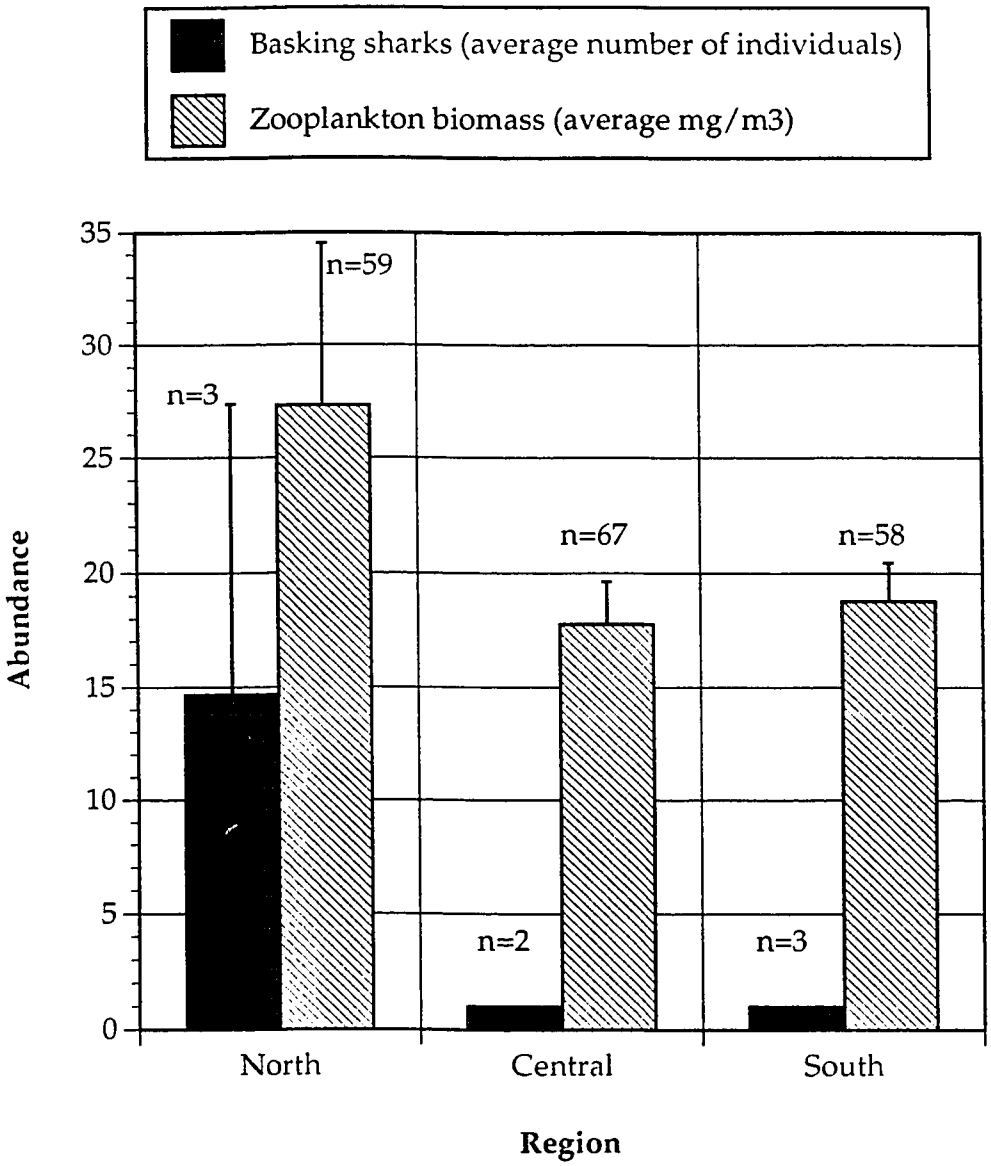

Fig. 26. Mean abundance of basking sharks (number of individuals) and zooplankton (mg/m3) among northern, central, and southern regions of Monterey Bay, California, from November 1991-August 1993. Standard error reported.

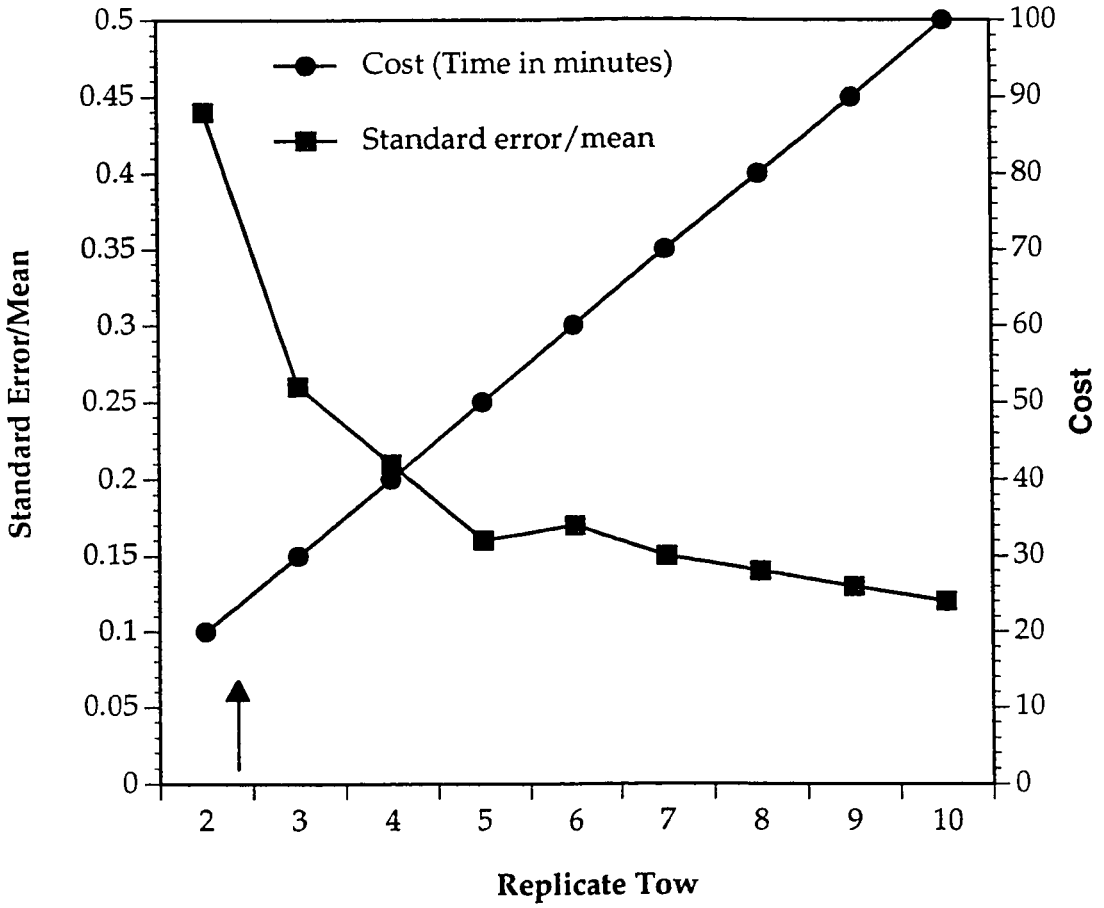

Fig. 27. Estimate of precision (SE/mean) for ten replicate tows conducted at one central nearshore station in Monterey Bay, California. Arrow indicates actual number of tows collected per station during the study period.

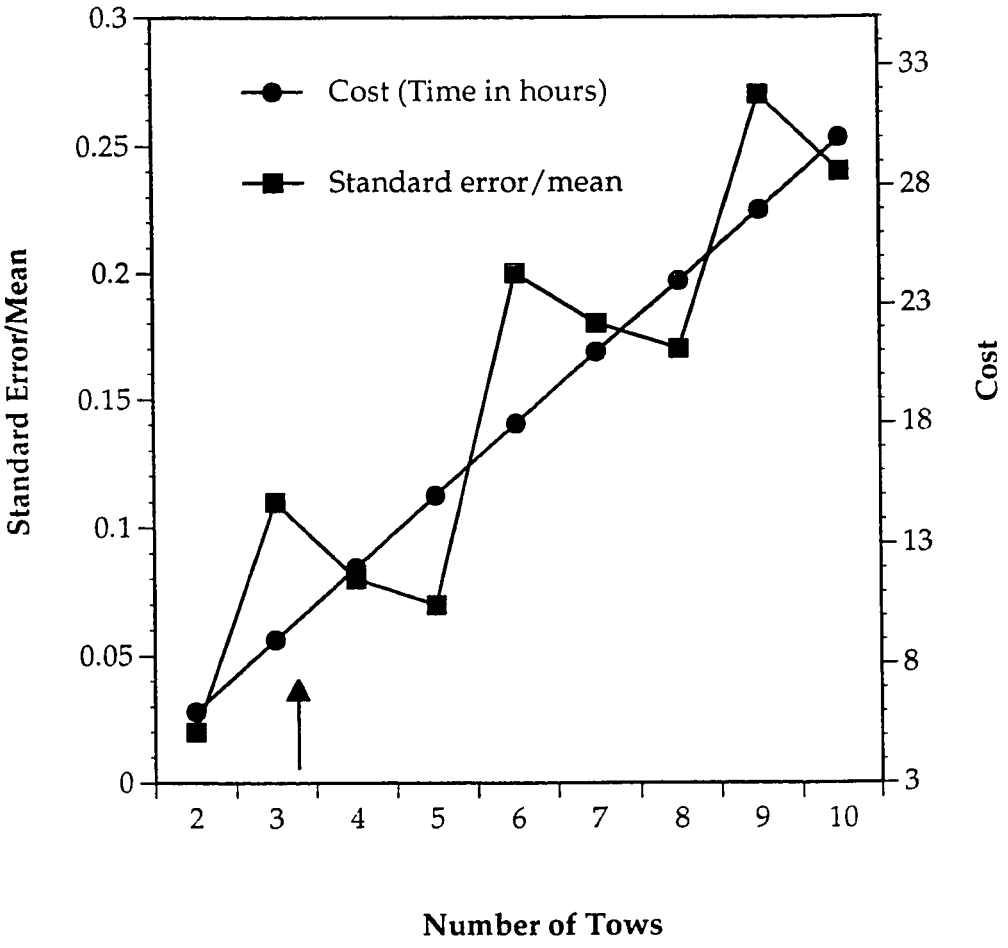

Fig. 28 . Estimate of precision (SE/mean) and cost (in time) for ten randomly allocated tows conducted among one central nearshore region of Monterey Bay, California. Arrow indicates actual number of tows collected per region during the study period.

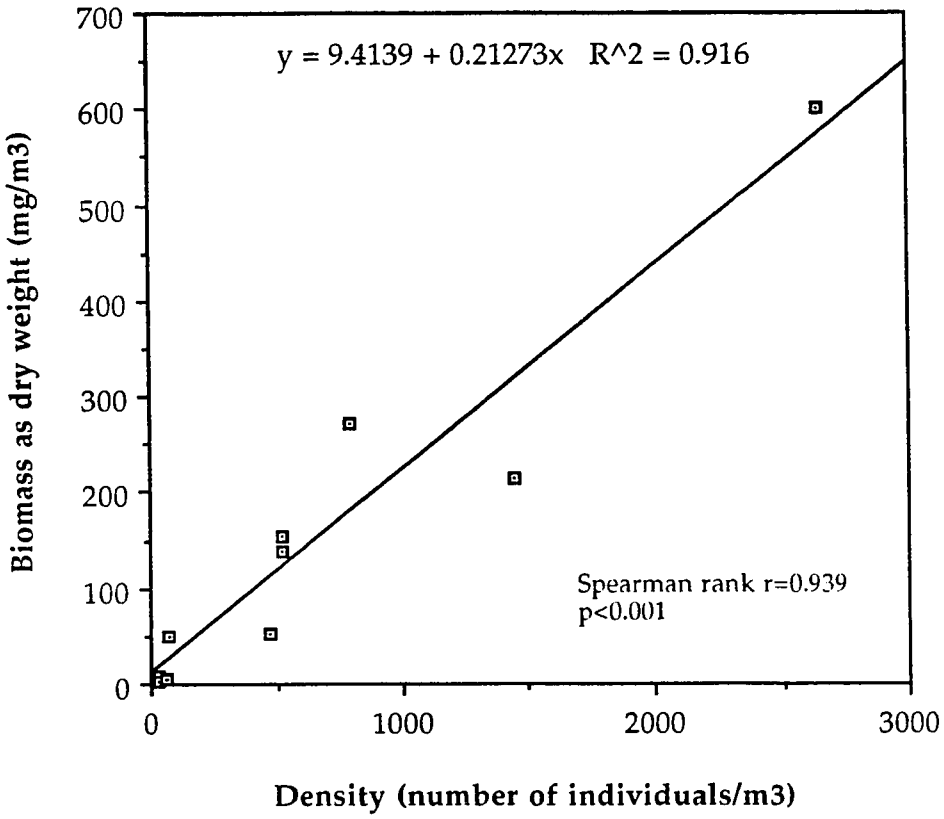

Fig. 29. Correlation between dry weight biomass (mg/m3) and density (number of individuals/m3) for zooplankton tows collected in Monterey Bay, California.

Appendix 1: Equations used to calculate Modified Index of Relative Importance (MIRI), Shannon-Weiner diversity, Dominance, and Zooplankton evenness.

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1. Equation for Modified Index of Relative Importance (IRI)

   IRI = (%Number + %Volume) * %Frequency of Occurence

   Modified IRI = (%N) * (%FO)

	Species A Number of indivuals/m^3	%N	%FO	IRI
Sample 1	20	25	25	625
Sample 2	10	15	25	375
Sample 3	0	0	25	0
Sample 4	15	23	25	575
Mean	11.25	15.75	25	**394**

2. Equation for Shannon-Weiner diversity (H')

   $H' = | (\Sigma p_i * \ln p_i) |$ $\quad p_i$ = proportion in sample

3. Equation for Dominance (D)

   $D = (\Sigma p_i^2)$

4. Equation for Zooplankton eveness (J)

   $J = H'/\ln S$

Appendix 2. Equations used to calculate Percent Similarity Index (PSI), Morisita-Horn Index of Similarity, and Horn's Index of Similarity.

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1. Equation for Percent Similarity Index (Renkonen 1938)

$P = \text{Sum minimum } (p1_i, p2_i)$

where P = Percentage similarity between samples 1 and 2

$p1_i$ = Percentage of species i in sample 1

$p2_i$ = Percentage of species i in sample 2

2. Equation for Morisita-Horn Index of Similarity (Morisita 1959)

$$C_\lambda = 2 \sum^{n} X_{ij} X_{ik} / (\lambda_1 + \lambda_2) N_j N_k$$

where C_λ = Morisita's index of similarity between samples j and k

X_{ij} X_{ik} = Number of individuals of species i in sample and sample k

$N_j = \Sigma X_{ij}$ = Total number of individuals in sample j

$N_k = \Sigma X_{ik}$ = Total number of individuals in sample k

3. Equation for Horn's Index of Similarity (Horn 1966)

$$R_o = \frac{\Sigma [(X_{ij} + X_{ik}) \log(X_{ij} + X_{ik})] - \Sigma (X_{ij} \log X_{ij}) - \Sigma (X_{ik} \log X_{ik})}{[(N_j N_k) \log(N_j + N_k)] - (N_j \log N_j) - (N_k \log N_k)}$$
